MISMATCH NEGATIVITY AS A MARKER OF AUDITORY PATTERN SEPARATION INTEGRITY IN AGING

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Abstract

How does auditory perception interact with precision in memory (i.e., mnemonic discrimination) in aging? This study examined how the mismatch negativity (MMN), an electrophysiological marker of change detection and encoding, relates to age differences in mnemonic discrimination. The MMN was recorded from 33 young (18–32 years, 18 females) and 30 older (55–86 years, 14 females) adults in a passive oddball paradigm using tone sequences. Participants then completed an incidental recognition test for old targets against similar lures and dissimilar foils. Older adults showed attenuated MMN amplitudes and poorer performance discriminating targets from lures and foils than young adults. Across participants, smaller MMN amplitude predicted worse recognition performance. Notably, MMN amplitude partially explained age-related declines in target-lure discriminability, but not target-foil discriminability. Findings reinforce the MMN as a marker of pattern separation integrity, and clarify how age-related declines in mnemonic discrimination are explained by age differences at encoding.

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Introduction

Healthy aging is accompanied by declines in episodic memory. In particular, older adults show declines in specificity and precision in memory, which may relate to compromised pattern separation—the neural process underlying the ability to distinguish separate, yet highly similar and overlapping events into discrete representations at encoding (Rolls, 2016). This finding has been well replicated across behavioural paradigms that test precision in memory (i.e., mnemonic discrimination) for studied target items to highly similar lure items. Studies using such tasks have shown preserved recognition for old items versus clearly new items in memory (e.g., identifying studied targets from unstudied foils, or the "old-new effect"), but disproportionate deficits in mnemonic discrimination in aging (Bowman et al., 2019; Stark et al., 2013, 2015; Stark & Stark, 2017; Toner et al., 2009; Yassa et al., 2011). Deficits in mnemonic discrimination are further exaggerated in individuals diagnosed with amnestic mild cognitive impairment (Reagh et al., 2014; Stark et al., 2013; Yassa et al., 2011), but are nonetheless a hallmark of healthy cognitive aging.

The neurocognitive basis of episodic memory decline in aging remains unclear, in part due to theoretical and methodological limitations from prior literature. For example, age-related deficits in memory may be explained by impairments at both encoding (i.e., acquisition of sensory input) and retrieval stages of memory (Cabeza et al., 1997; Craik & Rose, 2012; Langnes et al., 2019), as well as perceptual discrimination of stimuli (Clinard et al., 2010; Gellersen et al., 2021; Roberts & Allen, 2016). Furthermore, studies have shown neural evidence for age-related differences in the encoding of simple stimuli (e.g., pure tones) across multiple sensory domains (Alain et al., 2021; Reuter et al., 2013). As aging may affect perception as much as memory, it is possible that mnemonic discrimination difficulties observed in healthy older adults are explained

by age-related declines in perception at encoding. In other words, aging may be associated with deteriorated and less detailed representations of items at encoding in service of differentiating between old targets and highly similar lures. Moreover, past studies on mnemonic discrimination in aging are limited to the visual domain (Bowman et al., 2019; Davidson et al., 2019; Ly et al., 2013), and such deficits in the auditory domain have yet to be examined. The importance of this research is underscored given the associations between hearing loss and cognitive decline in aging (Fortunato et al., 2016; Uchida et al., 2019). Furthermore, studies of mnemonic discrimination tend to include familiar, everyday objects as stimuli (e.g., pictures of household items, fruits, etc.). These stimuli might mask age differences given older adults' propensity to rely on prior knowledge or gist to aid in learning and memory (Anderson et al., 2019; Duarte et al., 2010; Flores et al., 2017; Norman & Schacter, 1997; Tun et al., 1998). Therefore, the present thesis aimed to examine how perception at encoding relates to mnemonic discrimination deficits in aging—by examining if a neural index of change detection predicts the ability to discriminate learned from similar but unlearned items in memory. To account for the aforementioned limitations, we use a passive oddball paradigm that involves encoding of stimuli without conscious attention or instruction (i.e., incidental encoding) while using unfamiliar auditory tone sequences, as reported in our previous work in young adults (Herman et al., 2023).

Limited research has examined how mnemonic discrimination may be driven by perception in older adults. With behavioural measures, one study by Ly and colleagues (2013) showed marginally significant impairments in perceptual pattern separation of word stimuli in older adults as compared to young adults. Another study has shown that perceptual discrimination performance on oddity tasks for novel objects and scenes accounted for mnemonic discrimination performance in aging (Gellersen et al., 2021). Critically, findings from

Davidson and colleagues (2019) suggested some relationship between declines in visual perception and subsequent performance on the Mnemonic Similarity Task (MST), a task designed to assess pattern separation using pictorial stimuli of everyday objects. In this study, lure discrimination performance of older adults (but not those of young adults) was correlated with visual acuity. Interestingly, the correlation between lure discrimination and performance on neuropsychological tests of episodic memory no longer reached statistical significance once visual acuity was controlled for.

Studies using functional magnetic resonance imaging (fMRI) have also examined how brain activation patterns underlying visual perception at encoding accounts for subsequent precision in memory in young adults (Pidgeon & Morcom, 2016; Wing et al., 2020) and in older adults (Bowman et al., 2019). These studies show that neural activation patterns in visual regions at encoding (such as the ventral visual cortex and regions in midline occipital cortex) account for differences in subsequent mnemonic discrimination. In aging contexts, this research also demonstrates age-related reductions in fidelity of neural representations at encoding—possibly driven by age-related neural dedifferentiation (Koen, 2022; Zheng et al., 2018). However, these studies using fMRI are lacking in both temporal resolution and specificity to perception (such as accounting for individual or group differences in attention). Research with electrophysiological measures offer greater temporal resolution in measuring age differences at encoding. Here, studies investigating spatiotemporal patterns between encoding and retrieval (termed encoding-retrieval similarity, or ERS) have likewise found degraded, less distinctive neural representations of visual stimuli at encoding in aging (Lee et al., 2022; Sommer et al., 2019), although this research is again restricted to associative learning. Furthermore, despite these findings in the

visual domain, no study to our knowledge has investigated if perceptual processes at encoding predicts subsequent long-term episodic memory performance in the auditory domain.

Sensory-evoked potentials recorded by electroencephalography (EEG) can provide a sensitive neural representation of sensory input at encoding, in part due to its high temporal resolution and early latencies (Alain et al., 2021). In particular, the mismatch negativity (MMN), a robust electrophysiological waveform of deviance detection, can provide a an early index of encoding and auditory sensory memory (see Garrido et al., 2009 and Näätänen et al., 2007 for review). The MMN is commonly recorded using auditory event-related potentials (ERPs) that index context-dependent change detection. This ERP component is often elicited from violations of stimulus regularity, often from auditory oddball tasks, where a frequent repetitive stimulus (such as a pure tone) is occasionally replaced by an infrequent deviant stimulus that differs in some perceptual aspect, such as frequency, intensity, or duration. The MMN is computed by subtracting standard waveforms from deviant waveforms, thereby creating a difference waveform. The MMN presents itself when the waveform elicited by deviant trials is more negative in amplitude than by standard trials (hence the term “negativity”). This difference wave is apparent with changes in amplitude to sensory-evoked potentials, and has been demonstrated across different sensory modalities, including visual, olfactory, and somatosensory potentials (Näätänen et al., 2007). The MMN can be elicited even outside of conscious awareness, such as when participants are passively listening to stimuli, suggesting that bottom-up violations of stimulus regularity can occur at the pre-attentive level (Bartha-Doering et al., 2015; Sussman et al., 2003). Both amplitude and latency of the MMN has been shown associations with perceptual discrimination ability. For example, its amplitude is larger, and its latency occurs earlier with a larger difference in acoustic change between standard and deviant stimuli (Näätänen & Alho,

1997; Schröger et al., 1992). As well, an earlier MMN latency has been shown to predict faster behavioural responses to change detection (Tiitinen et al., 1994). A strength of this electrophysiological measure is its independence from the direction of attention; the MMN does not require overt attention or behavioural responses to be elicited, and its amplitude has been shown to be stable regardless of whether participants attend to or ignore the stimuli, so long as the context of the stimuli remain task-irrelevant (Näätänen et al., 2007; Sussman et al., 2003, 2014). Therefore, this neural marker can provide an objective index of the encoding of auditory sensory input, especially in non-attentive, incidental contexts.

The MMN is especially suitable for examining the influences of incidental encoding on subsequent memory, and particularly useful in aging contexts given age-related differences in attentional orienting (Alain et al., 2018; Greenwood & Parasuraman, 2004) and sustained attention (Carriere et al., 2010; Staub et al., 2015). Research has largely shown reductions in MMN amplitude in healthy aging, possibly indicating impairments in auditory sensory memory (Cheng et al., 2013; Cooper et al., 2006; Ruzzoli et al., 2012) via age differences at encoding (Näätänen et al., 2005). One study posited that auditory sensory memory rather than encoding is impaired in aging, finding no difference in MMN amplitude between young and older adults for short ISIs (400 ms) and absent MMN in older adults at longer ISIs (4000 ms, Ruzzoli et al., 2012). However, other research has shown smaller MMN amplitudes in older adults across short and long inter-stimulus intervals (ISIs) compared to young adults (Alain & Woods, 1999; Cooper et al., 2006; Czigler et al., 1992; Karayanidis et al., 1995; Pekkonen, 2000), providing neural evidence for degraded sensory input at encoding. Indeed, a meta-analysis by Cheng and colleagues (2013) of 165 older adults and 182 young adults showed prominent age-related attenuations in MMN amplitudes (with an overall moderate effect size of 0.63) across short and

long ISIs and across different stimulus deviance manipulations (i.e., across temporal duration and pitch frequency changes). Whether these age-related attenuations in MMN amplitude accompany concurrent declines in episodic memory in aging has yet to be studied.

Taken together, the aim of this study was to examine the extent to which perception at encoding, as indexed by the MMN, contributes to age-related deficits in episodic memory (and particularly, mnemonic discrimination) in the auditory domain. To this end, the MMN was recorded in young and older adult participants using a passive auditory oddball paradigm of standard and deviant tone sequences (differing in pitch contour but matched for mean frequency). Prior studies have used similar stimuli differing in pitch contour to elicit the MMN (Alain et al., 1998, 1999; Fujioka et al., 2004; Tervaniemi et al., 2001, 2006; Trainor et al., 2002; see Paavilainen, 2013 for review). Participants were then presented with an incidental old/new recognition test that included the same tone sequences (i.e., targets), intermingled with similar lures and dissimilar foils. In our recent work with young adults using the same paradigm (Herman et al., 2023), the amplitude of the MMN was found to be correlated with ability to discriminate targets from lures, but not targets from foils. Whether this finding may also extend to older age, or whether age mediates the relationship between MMN and lure discrimination, remains to be examined. From prior research, we expected that 1) older adults would demonstrate attenuated amplitudes in the MMN amplitude compared to young adults. Next, given that the MMN from this paradigm is thought to index incidental encoding, we also hypothesized similar with Herman and colleagues (2023) that 2) the MMN would be correlated with deficits in mnemonic discrimination (i.e., between targets and lures) when also including data from older adults. These analyses were followed up by regression models to examine whether MMN amplitude had unique predictive value in accounting for memory performance

above and beyond age. Finally, given that aging is associated with declines in mnemonic discrimination, we hypothesized that 3) perception at encoding would be a mediating factor in explaining the relationship between older age and declines in memory discriminability. To this end, mediation analyses clarified the extent to which incidental encoding (as measured by the MMN amplitude) contributes to age-related declines in memory, particularly for mnemonic discrimination.

Methods

Participants

Young adults were recruited from the York University undergraduate research participant database and through the local community. Older adults were recruited from the Rotman Research Institute participant database, as well as through online advertisements and community talks in the Greater Toronto Area of Ontario, Canada. Young adult participants were provided with course credit for their first-year undergraduate introductory psychology course or monetary compensation, and all older adults received monetary compensation. Inclusion criteria for all participants included self-reported fluency in English, and absence of neurological conditions (including stroke, transient ischemic attack, or traumatic brain injury), formal psychiatric diagnoses, substance use disorder, and learning disabilities. Participants were excluded if they were undergoing chemotherapy, radiation therapy to the head or neck, or concurrently taking medications known to affect cognitive functioning (such as antidepressant or antipsychotic medications). Further exclusion criteria included concurrent use of hearing aids or reporting hearing difficulties. These young adults comprised the same sample reported in Herman et al., (2023). Additionally, all older adult participants had not undergone neuropsychological

assessment within six months prior to testing, and the subset of participants older than 60 years scored above the cut-off on the modified version of the Telephone Interview for Cognitive Status-modified (TICS-m) to ensure absence of significant cognitive impairment.

As recruitment of older adults formed part of a larger study examining the effect of musical training on mnemonic discrimination, data from older musicians were excluded from the analysis to represent the general older adult population. These included individuals who had studied or obtained professional degrees in musical performance or music education; and those who had five or more years of formal music lessons on an instrument that extended beyond general academic curricula and were currently practicing or playing an instrument at the time of testing (Zhang et al., 2020).

Clinical pure-tone audiograms were administered to all participants to ensure a normal hearing profile and hearing acuity expected for their age group. All young participants demonstrated typical bilateral pure-tone thresholds that fell below 25 decibels (dB) hearing level (HL) across each octave of frequency from 250 to 8000 Hz. Three older adults were excluded from the study due to moderate hearing loss exceeding 35 decibels (dB) hearing loss (HL) averaged from 250 to 2000 Hz bilaterally. Another older adult was excluded from the study due to asymmetrical bilateral hearing acuity. All included participants reported correct or corrected-to-normal vision. Data from two young adults and five older adults were excluded from analysis for failing to understand task instructions, and data from one young adult and one older adult were excluded for falling asleep during the majority of the EEG recording. As stimuli from the main task of interest were tone patterns differing in pitch contour, data from four young adult participants were excluded from analysis as they demonstrated below-chance level pitch contour discrimination, as measured in the back-to-back discrimination phase of the experimental

protocol. The final sample of participants included 30 young adults (18–32 years, 18 females) reported from Herman et al., 2023, and 33 older adults (55–86 years, 14 females). The groups did not statistically differ by sex, χ^2 (1, N= 63) = 1.942, p = .163. Sample size was approximated and informed based on data from correlation plots between the MMN and working memory in older adults reported in Bonetti and colleagues (Bonetti et al., 2018). Using G*Power (Faul et al., 2009), 29 participants per group would be adequate in detecting a significant correlation between MMN amplitude and a measure of cognitive performance given r = .45, α = .05, and 1-β = .80. The experimental protocol was approved by the Research Ethics Boards of York University and the Rotman Research Institute at Baycrest Centre, and all participants provided informed written consent.

Neuropsychological Assessment

The Montreal Cognitive Assessment was administered to all older adult participants as a brief measure of global cognitive ability. Participants were also administered the Generalized Anxiety Disorder Scale (GAD-7) and the Patient Health Questionnaire (PHQ-8) to assess concurrent anxiety and depressive symptoms. Older adults over 60 years of age were administered additional neuropsychological tests to ensure cognitive functioning expected for their age. The Wechsler Abbreviated Scale Intelligence (WASI) Vocabulary and Matrix Reasoning subtests were administered as abbreviated measures of crystallized and fluid intelligence, respectively. The Wechsler Adult Intelligence Scale, 3rd edition (WAIS-III) Digit Symbol Coding subtest and Trails A of the Trail-Making Test were administered as measures of processing speed, while Trails B provided a measure of inhibitory control and cognitive flexibility. Memory was assessed using the California Verbal Learning Test II (CVLT-II) and the Incidental and Free Recall sections of the Digit Symbol Coding Test. The Digit Span subtest of

the WAIS-IV was administered to assess auditory short-term and working memory. The Delis-Kaplan Executive Function System (D-KEFS) Verbal Fluency subtest was administered to assess phonemic and semantic fluency. Finally, as the stimuli used in the present study varied in pitch contour, the Musical Ear Test was administered to assess levels of musical acuity in both melodic and rhythmic domains.

Procedure

All participants completed two computerized tasks of mnemonic discrimination. To ensure our sample of older adults demonstrated mnemonic discrimination performance similar to older adult samples from prior research, participants completed the MST (Stark et al., 2013), a task of visual mnemonic discrimination for everyday objects, and has been considered a robust behavioural marker of pattern separation integrity. Participants then completed the main experimental task, named the Auditory Pattern Separation Task (APST), a novel task of mnemonic discrimination for unfamiliar auditory stimuli. All participants completed the MST first and the APST second, and were given the option for breaks in between tasks. Older adults over 60 years of age completed the MST and APST on a separate day from neuropsychological assessment to prevent fatigue, all of whom completed both testing sessions within two months. No data from any older adult participant were lost due to attrition.

Mnemonic Similarity Task

The MST was given to all participants as a pre-test to ensure comparable mnemonic discrimination abilities as compared to samples from prior literature. The MST comprises two phases: an incidental encoding phase and a recognition test phase. In the encoding phase, participants make judgements of 128 pictures of everyday objects as to whether each are

categorized as indoor or outdoor objects. Immediately afterwards, the test phase follows, where participants are presented 192 images of everyday objects, and identify each object as “old”, “similar”, or new” relative to the encoding phase. Stimuli in the test phase were the same pictures presented in the encoding phase (i.e., targets), pictures not previously seen in the encoding phase (i.e., foils), or pictures that were perceptually similar but not identical to those presented in the encoding phase (i.e., lures). Participants completed the MST following established protocol (Stark et al., 2013) and were randomly assigned one of two analogous stimulus sets (Set C or D). Participants responded to each picture stimulus by pressing a key on a computer keyboard. Young adults completed the MST on a Windows 7 laptop in a quiet testing room in the absence of the experimenter, while older adults completed the MST via a desktop computer in a double-walled sound-attenuated booth. The visual stimuli of the pictures of everyday objects in both encoding and test phases are presented at 2 s each, with an inter-stimulus interval (ISI) of 500 ms.

Auditory Pattern Separation Task

Figure 1 shows a schematic of the APST. The APST comprises three stages: an incidental encoding phase, a forced-choice recognition test phase, and a back-to-back discrimination phase. Details regarding the generation of these stimuli have been previously reported in Herman et al. (2023). Stimuli were auditory tone sequences, each comprising five pure-tones 100 ms in length. The APST used six different tone sequences differing in pitch contour with the frequency distribution for each stimulus type shown in Figure 2. Only two stimulus types (a standard and deviant) were presented in the encoding phase, and all six stimulus types were presented in the following phases. Auditory stimuli were presented through Etymotic ER-3A insert earphones (Etymotic Research, Elk Grove, IL, USA), and the sound intensity was set at 85 dB sound

pressure level (SPL). All participants completed the APST while seated in a recliner in a double-walled sound-attenuated booth.

Encoding Phase and EEG Acquisition

Two types of auditory tone sequences (a standard and a deviant) were presented sequentially in a randomized order while participants watched a silent film for 25 minutes. Participants were instructed to attend to the film, and an experimenter monitored the testing session from outside the sound booth via a webcam to ensure participants complied with experimental protocol. In this paradigm, a standard pure-tone sequence is presented for 700 trials, and a deviant sequence is presented for 300 trials. Each tone sequence, which lasted 500 ms in length from stimulus onset to offset, was separated by a jittered ISI between 900 to 1150 ms (50 ms step, rectangular distribution). These tone sequences were designed to be similar in mean frequency, but discriminable in pitch contour.

Meanwhile, EEG was recorded from 66 Ag/AgCl scalp electrodes using a BioSemi ActiveTwo acquisition system (BioSemi V.O.F., Amsterdam, Netherlands). The electrode montage followed the international 10-20 system, and reference electrodes comprised a common mode sense active electrode and driven right leg passive electrode serving as ground. Ten additional electrodes were added and placed below the hair line to monitor eye movements and to cover the whole scalp evenly. These electrodes were placed at both mastoids, bilateral pre-auricular points, lateral points beside the outer canthus of each eye, and inferior to the orbit of each eye, along with two additional frontotemporal electrodes. EEG data were digitized continuously at a rate of 512 Hz with a bandwidth of direct current (DC) of 100 Hz, and then stored offline for analysis.

Test Phase

Following the encoding phase, participants were probed with same standard and deviant tone sequences previously presented (i.e., targets) intermixed with lure and foil sequences. To ensure the test phase placed demands on long-term memory rather than working memory or sustained attention, the test phase followed the encoding phase after two to three minutes where participants took a break and received instructions from experimenters. Participants were then instructed to respond to whether or not each tone sequence (i.e., probe) was previously presented in the encoding phase via a key press on a computer keyboard. Target stimuli were the same standard and deviant tone sequences from the encoding phase, which were presented amidst unfamiliar tone sequences (i.e., lures and foils). Of these stimuli, three different auditory sequences were designated as lures, and one auditory sequence was designated as a foil. Lure stimuli were designed to be similar in mean frequency, but discriminable in pitch contour relative to target sequences. In contrast, the foil stimulus type was designed to be dissimilar in both domains. During the test phase, the six stimulus types (i.e., two targets, three lures, and one foil) were each probed ten times in a randomized order, amounting to 20 target trials, 30 lure trials, and 10 foil trials for a total of 60 trials. The test phase was self-paced, and included a 500-ms interval between stimulus presentation and instruction probe.

Discrimination Phase

Following the test phase, a back-to-back discrimination phase was administered to ensure participants could discriminate between stimulus types. This post-test was not a primary outcome of interest in the present study; performance here and was used only to ensure that participants could perceive targets, lures, or foils as distinct from each other during retrieval in the earlier test

phase. For each trial, a pair of tone sequences was played sequentially with an ISI of 500ms between each pair. Participants reported with keypress whether the successive tone sequences were the same or different. Each tone sequence was presented with itself and with every other tone sequence, requiring 84 trials from 42 unique pairs of tone sequences presented in each order. The task is forced-choice and self-paced, and participants respond via a key press on a computer keyboard.

Data Preparation

EEG Preprocessing

All ERP preprocessing stages were performed using Brain Electrical Source Analysis (BESA) software (BESA Research, version 7.1, MEGIS GmbH, Gräfelfing, Germany). Continuous EEG data were averaged referenced, then digitally filtered with 0.53 Hz high-pass (forward, 6 dB/octave) and 40 Hz low-pass filters (zero phase, 24 dB/octave) to correct for artifacts at low delta band or high gamma frequency bands. Individual channels showing excessive artifacts and drift, such as those attributed to head or body movements, were interpolated using spherical spline interpolation (Picton et al., 2000), with no more than 10% of channels per recording interpolated. For each participant, a set of ocular movements were identified from the continuous EEG recording based on the spatial components approach of correcting eye artifacts (Berg & Scherg, 1994; Ille et al., 2002), and were then used to generate spatial components that best account for eye movements. The spatial topographies were then subtracted from the continuous EEG to minimize contaminations from eye-blinks, and lateral and vertical eye movements. After correcting for eye movements, data for each participant were then segmented into epochs of 0 ms to 1000 ms with a baseline of -200ms to 0ms. Epochs were

then scanned for additional artifacts, with epochs including deflections exceeding above or below a 60 μV difference between the maximum and the minimum amplitude for a given trial and channel marked and excluded from the analysis. For young adults, this excluded on average 7.58% (*SD* = 5.12%) of standard trials per participant, and 7.88% (*SD* = 5.48%) of deviant trials per participant. For older adults, this excluded on average 9.26% (*SD* = 8.23%) of standard trials per participant, and 9.49% (*SD* = 8.38%) of deviant trials per participant; these did not differ between groups, $F(1, 61) = .88$, $p = .351$, $\eta_p^2 = .014$. The remaining epochs were averaged according to experimental conditions (i.e., standard and deviant), and averaged epochs were baseline-corrected with respect to the pre-stimulus interval (i.e., mean amplitude over the 200 ms prior to stimulus onset to prevent contamination from preceding trials). The MMN difference waveform was then computed for each participant by subtracting deviant from standard waveforms.

Behavioural Measures

For the MST test phase, trials without a response after the response time window of 2500 ms were discarded from analysis. To account for accidental button presses, trials with responses less than 400 ms were also discarded from calculations of accuracy. Accuracy rates were calculated for each response bin (i.e., proportion of targets correctly responded as “old”, proportion of lures correctly responded as “similar”, and proportion of foils correctly responded as “new”). Two measures of interest were the traditional recognition score (TRS) and the lure discrimination index (LDI). The TRS is a commonly used index of recognition performance for the “old-new” effect in episodic memory, given by hit rates for targets (i.e., responding “old” to studied items) minus false alarms for foils (i.e., responding “old” to unstudied items). The LDI

indexes mnemonic discrimination performance and is given by the rates of responding to lure objects as similar minus responding to foil objects as similar (i.e., similar | lure – similar | foil).

As the APST test phase provides only two response options for participants, this allows for calculation of signal detection measures. Two outcome measures of interest were target-foil discriminability (as a traditional measure of old-new recognition, calculated by z(old | targets) minus z(old | foil)), and target-lure discriminability (as a measure of mnemonic discrimination, calculated by z(old | targets) minus z(old | lures)). Each were measured through loglinear d-prime from signal detection theory using the Hautus (1995) adjustment for extreme values; A-prime metrics were also calculated and used in correlation analyses as a supplementary measure for convergent validity. These measures were calculated in using the *psycho* package (Makowski, 2018).

For the back-to-back discrimination phase of the APST, accuracy for same trials, different trials, and overall accuracy were calculated. As mentioned previously, two young adult participants scored below chance level for the discrimination phase, and their data were subsequently excluded from analysis. All preprocessing of behavioural data was conducted using R software (version 4.2.3).

Data Analysis

Mismatch Negativity

Based on visual inspection of the data, two negative deflections in deviant waveforms (relative to standard waveforms) were observed. One negativity was elicited 200–400 ms which occurred after stimulus onset and before stimulus offset, and was therefore labelled and identified as the MMN. Another negativity was apparent 550–700 ms after stimulus onset after

stimulus offset, was therefore labelled and identified as a late discriminative negativity (LDN). Given that the latency of the LDN occurred after stimulus offset, the functional significance of this ERP fell outside the scope of perception, and will be analyzed elsewhere.

Cluster-based permutation testing was performed to statistically quantify and confirm the presence of the MMN in both age groups through a data-driven approach. Two-tailed permutation t-tests were conducted: a) one paired-samples t-test between standard and deviant trials within young adults, and b) one paired-samples t-test between standard and deviant trials within older adults. Furthermore, to statistically quantify the group difference in MMN and LDN amplitudes, c) an independent-samples t-test for MMN difference waveforms between age groups was conducted. EEG data were analyzed with BESA Statistics software (BESA Statistics, version 2.0, MEGIS GmbH, Gräfelfing, Germany). This software allows for data-driven statistical tests on amplitude waveforms across all scalp electrodes and can perform permutation t-tests and topographic ANOVAs while accounting for alpha inflation from multiple comparisons.

Each permutation t-test comprised two phases of analysis. In a preliminary phase, amplitude waveforms per participant were analyzed between groups using parametric t-tests at each pair of sensors (within-subjects t-tests when comparing standard and deviant conditions within each age group; between-subjects t-tests when comparing difference waveforms between age groups). Clusters of contiguous data points falling below a cluster-building alpha of $p < 0.05$ were derived. For each spatiotemporal cluster, the sum of t-values of sampling points within each cluster then formed the cluster-level statistics (referred to as cluster values). In the subsequent analysis phase, permutation testing was conducted using a Monte-Carlo resampling technique, which involves comparing the observed cluster value with random cluster values drawn from a

permutation distribution. This permutation distribution was created by randomly assigning levels of the factor of interest (either group or condition) and repeatedly conducting the same test many times (in this paper, 5000 random permutations), retrieving the maximum cluster value with every permutation. The largest absolute cluster value was subsequently compared to the permutation distribution of maximal cluster values. If the maximum cluster value from the observed data is larger than 95% of the maximum cluster values in the permutation distribution, then the null hypothesis (i.e., that the two groups, or two conditions, are sampled from the same distribution) is rejected (Maris & Oostenveld, 2007). In summary, cluster-based permutation testing identifies spatiotemporal clusters (specifying an array of electrodes and a time window) that differ between groups or between conditions. Each cluster represents an amplitude modulation with an associated Monte-Carlo *p*-value that represents the proportion of randomized permutations where the observed cluster value is larger than the value drawn from the permutation distribution. For an in-depth overview of permutation statistics as implemented in BESA Statistics software, see Maris and Oostenveld (2007).

Behavioural Measures

LDI and TRS indices from the MST were subjected to independent-samples t-tests between groups. As for the APST test phase, d-prime and A-prime indices for each of target-lure and target-foil discriminability were subjected to an independent-samples t-test between groups. Finally, a mixed ANOVA was conducted on APST hit rates with Group (young, older) as a between-subjects factor and Condition (target, lure, foil) as a within-subjects factor.

As for the APST discrimination phase, hit rates for overall, different, and same stimulus pairs were calculated. Given non-normal distributions for each of these three measures (as shown by Shapiro-Wilk tests, each $p < .001$), non-parametric Mann-Whitney U tests were conducted.

All ANOVAs were run with Sidak correction to correct for multiple comparisons. A Greenhouse-Geisser correction was used to correct for violations of sphericity, and partial-eta squared was reported as a measure of effect size.

Correlation Analyses

Two-tailed bivariate Pearson correlations were conducted between MMN mean amplitude and LDN mean amplitude on one end, and subsequent memory performance on the other (i.e., d-prime for target-lure or target-foil discriminability, with A-prime as a supplemental measure). Exploratory correlation analyses were also conducted between age in years and each of the neural and behavioural measures mentioned previously. As the MMN largely tends to be maximal at frontal and frontocentral electrode sites, the mean amplitudes of the MMN for each participant were derived from a cluster of seven electrodes from frontal and frontocentral sites (AFz, F1, Fz, F2, FC1, FCz, FC2) averaged across a time window informed by visual inspection and permutation testing. Correlation coefficients are also reported with bias-corrected accelerated 95% confidence intervals (BCa CIs) using 1000 bootstraps. Since MMN and LDN amplitudes are largely negative (hence the term negativity), larger MMNs and LDNs signify greater amplitude of the ERP. Therefore, values for both MMN and LDN measures have reversed its sign (i.e., positive to negative, and vice versa) for ease of interpretation. A positive correlation coefficient would thus signify that a larger MMN or LDN amplitude is associated with better discriminability.

Regression and Mediation Analyses

Hierarchical regression models were also conducted to examine whether MMN amplitudes predict subsequent memory performance (d-prime measures) above and beyond age, as well as whether age moderates the strength of the relationship between MMN and subsequent memory performance. MMN amplitude was entered as the sole predictor in a regression model, followed by age added as another predictor in examining whether the MMN holds as a significant predictor of target-lure and target-foil d-prime measures. Standardized regression coefficients are reported, and the standard errors and BCa CIs were obtained through bootstrapping with 5000 iterations. Finally, mediation analyses were conducted to examine indirect effects from the regression model regressing age on each of lure discriminability and foil discriminability, with MMN amplitude as a simple mediator (simple mediation model). Unstandardized path coefficients are reported with bias-corrected 95% CIs bootstrapped with 5000 iterations. All analyses involving behavioural data were run using IBM SPSS (version 28) and JASP (version 0.17.1).

Results

Neuropsychological Measures

Demographic and neuropsychological data are outlined in Table 1. The older adult sample was highly educated (16.58 years, *SD* = 2.14 years), and showed average to high average scores on tests of episodic memory, as well as high average to above average scores on tests of processing speed and executive functioning.

Event-Related Potentials

Figure 3 shows standard and deviant grand-averaged waveforms and the resulting difference waveform for each group. Figure 4 shows sample waveforms across the cluster of seven frontal and frontocentral electrodes. As expected, the first tone of each auditory sequence elicited a P1-N1-P2 complex, a hallmark of the frontocentral auditory-evoked potential (Alain, Cortese, et al., 1998; Picton, 2010). The N1 corresponding to each of the four subsequent tones were also visible in both standard and deviant waveforms; these early sensory potentials were visible in both young and older adult groups. The presence of the MMN and LDN for each group was identified through visual inspection and then statistically verified in each group via permutation testing. The MMN was identified in both young and older adult groups as a prominent early frontal negativity (~200–400ms) in deviant compared to standard trials before the offset of the pure-tone sequence. Permutation testing similarly verified the presence of the MMN at frontal and frontocentral electrodes, as well as its polarity reversal spanning lateral and temporal electrodes. The LDN was also identified through visual inspection via a later frontal negativity (~500–750ms) in deviant compared to standard trials but occurring after stimulus offset. Similarly, permutation testing confirmed and statistically quantified the presence of the LDN at frontal and frontocentral electrodes, as well as its polarity reversal spanning lateral and temporal electrodes. Based on visual inspection and permutation testing on grand-averaged waveforms, mean amplitudes for each participant were averaged across 200–400 ms for the MMN for the purposes of correlation and regression analyses. Cluster-based statistics for the amplitude difference between standard and deviant trials are shown in Table 4 for younger adults and Table 5 for older adults.

To statistically quantify the group difference in MMN amplitude, permutation testing was also conducted on difference waveforms between young and older adults. Analyses confirmed, in

older adults, smaller MMN amplitudes at frontal and frontocentral electrodes, as well as a smaller amplitude for its polarity reversal at lateral-temporal electrodes compared to young adults. Table 6 shows the cluster-based statistics for the group comparison of difference waveforms.

Results of permutation testing were verified by independent-samples t-tests between groups for MMN amplitude values used in the correlation and regression analyses (i.e., values averaged over 200–400ms time window, across seven frontal and frontocentral electrodes). As expected, older adults showed smaller MMN amplitudes compared to young adults, $t(41.93) = 4.436$, $p < .001$, *Cohen's d* = 1.152).

Behavioural Measures

MST Performance

Table 2 shows proportion endorsed per stimulus and response type, and Figure 5 shows the LDI and TRS scores for each group. Analysis was conducted on a subset of 31 older adults; one older adult did not complete the MST due to self-reported colour-blindness, and data from another older adult were outliers on both LDI and TRS metrics. As expected, older adults showed lower LDI scores compared to young adults, $t(60) = 4.410$, $p < .001$, *Cohen's d* = .292, and no group difference in TRS scores was found, $W = 493.50$, $p = .855$, $r_{rb} = .028$. In summary, our older adult sample showed selective impairments in mnemonic discrimination but spared "old-new" episodic memory compared to young adults. LDI scores for the present older adult sample ($M = .13$, $SD = .20$) were comparable to those from the older adult sample ($n = 94$) reported in Pishdadian et al. (2020) with ($M = .14$, $SD = .13$; $t(125) = .017$, $p = .866$).

APST Recognition Performance

Figure 6 shows hit rates by condition for each group. Results from the mixed ANOVA showed a Group main effect, $F(1, 61) = 59.42$, $p < .001$, $\eta_p^2 = .493$, and a Condition main effect, $F(1.75, 106.53) = 54.75$, $p < .001$, $\eta_p^2 = .473$. The Group by Condition interaction, however, did not reach significance, $F(1.75, 106.53) = 2.00$, $p = .146$, $\eta_p^2 = .032$. Post-hoc tests demonstrated that lure endorsement was significantly poorer than hit rates for either targets ($p < .001$) or foils ($p < .001$).

As for discriminability measures, older adults showed poorer target-lure discriminability ($t(59.64) = 7.502$, $p < .001$, *Cohen's d* = 1.898 for d-prime; $t(44.47) = 7.19$, $p < .001$, *Cohen's d* = 1.784 for A-prime) and poorer target-foil discriminability ($t(49.01) = 5.901$, $p < .001$, *Cohen's d* = 1.468 for d-prime; $t(35.22) = 7.502$, $p < .001$, *Cohen's d* = 1.895 for A-prime) compared to young adults.

APST Discrimination Phase

Table 3 shows hit rates for the back-to-back discrimination phase. Both young and older adults showed high overall discrimination rates averaged across the 21 stimulus pairs in this post-test, with young adults approaching ceiling-level performance rates for discriminating repeated stimulus pairs as "same" and discriminating different stimulus pairs as "different". Only two older adults showed below chance-level discrimination rates (<50%) for discriminating different pairs, and were above chance on discriminating repeated stimulus pairs. Older adults showed lower discrimination rates in older than young adults for overall discrimination rates ($W = 851$, $p < .001$, $r_{rb} = .719$) and for discriminating different stimulus pairs ($W = 855.5$, $p < .001$, $r_{rb} = .728$), but no group difference in discriminating repeated pairs ($W = 544$, $p = .448$, $r_{rb} = .099$).

Correlation Analyses

Table 7 shows the correlation matrix between age, MMN, LDN, target-lure discriminability, and target-foil discriminability across all participants. Consistent with findings with only the young adult sample in Herman and colleagues (2023), MMN amplitude was significantly correlated with d-prime for lure discrimination, r = .558, BCa CI [.361, .709], p < .001 (Figure 7A). MMN amplitude was also significantly correlated and foil discrimination, r = .298, BCa CI [.108, .474], p = .018 (Figure 7B). A two-tailed Fisher's z-test for dependent samples showed that the relationship of the MMN with lure discriminability and foil discriminability differed in strength, z = 2.837, p = .002, consistent with the idea that lure discriminability and foil discriminability represented distinct constructs. When running the same analysis using A-prime as a supplementary measure, we confirmed that the MMN was again significantly related to lure discrimination, r = .452, BCa CI [.293, .584], p < .001, and marginally significantly correlated with foil discrimination, r = .227, BCa CI [.079, .370], p = .079. These correlations were also significantly different from another, z = 2.044, p = .020.

As expected, older age was also significantly correlated with decreased MMN amplitude, r = .515, BCa CI [.325, .668], p < .001, poorer target-lure discriminability (r = -.702, BCa CI [-.584, -.795], p < .001 for d-prime; r = -.664, BCa CI [-.543, -.767], p < .001 for A-prime), and poorer target-foil discriminability (r = -.644, BCa CI [-.499, -.773], p < .001 for d-prime; r = -.577, BCa CI [-.437, -.701], p < .001 for A-prime). Surprisingly, three older adults incorrectly endorsed nine of the 10 presentations of the foil probe as "old", and two more older adults incorrectly endorsed all 10 presentations of the foil as "old". Data from these individuals were not identified as outliers on either lure endorsement or foil endorsement. Nevertheless, the same

pattern of results was found for foil discrimination when replicating analyses without these five data points.

Exploratory correlations were also run between LDN amplitude, age, and memory performance. No correlation between LDN amplitude and d-prime measures reached significance (r = .046, p = .721 for lure discrimination; r = .094, p = .464 for foil discrimination). LDN amplitude and age were also not significantly correlated with each other, r = -.029, p = .821.

In summary, the correlation analyses showed significant correlations between each of age, MNN amplitude, target-lure discriminability, and target-foil discriminability. Exploratory analyses showed no significant correlations with LDN amplitude with either age or memory performance.

Regression Analyses

A hierarchical regression model was run to examine whether MMN amplitude significantly predicts lure discrimination (d-prime measures only) above and beyond the predictive value of age. Results of the regression models are shown in Table 8 for target-lure discriminability and Table 9 for target-foil discriminability. The regression model that included MMN as the only predictor reached significance, $F(1, 62) = 27.63$, $p < .001$, $R^2 = .312$, where $\beta = .558$. The next regression model that included both MMN and age as predictors also reached significance, $F(2, 62) = 36.00$, $p < .001$, $R^2 = .545$. Age ($\beta = -.564$, $p < .001$) was a significant predictor of lure discrimination, and MMN amplitude remained a significant predictor ($\beta = .268$, $p = .011$). The addition of age into the regression model significantly improved the model's predictive value with lure discrimination, $F(1, 60) = 30.86$, $p < .001$, $\Delta R^2 = .234$.

A regression model with the same predictor variables was run for foil discrimination (d-prime measures). The model that included MMN as the only predictor reached significance, $F(1, 62) = 5.928$, $p = .018$, $R^2 = .089$, where $\beta = .298$. Next, the regression model that included MMN and age also reached significance, $F(2, 62) = 25.28$, $p < .001$, $R^2 = .416$. Age ($\beta = -.667$, $p < .001$) was a significant predictor of foil discrimination, and MMN amplitude was no longer a significant predictor ($\beta = -.046$, $p = .590$). The addition of age into the regression model significantly improved the model's predictive value with foil discrimination, $F(1, 60) = 33.60$, $p < .001$, $\Delta R^2 = .327$. The same pattern of results was found for this regression model when replicated without data from the five older adults who endorsed nine or more of the 10 foil probes as "old". In summary, MMN amplitude predicted lure discrimination above and beyond the predictive value of age, whereas the relationship between MMN amplitude on foil discrimination was better explained by the age.

Mediation Analyses

Figure 8 shows a schematic of the simple mediation model for both lure discrimination and foil discrimination. For lure discrimination, results showed that the direct effect of age on lure discrimination was significant ($B = -.022$, $SE = .004$, $p < .001$, 95% CI [-.030, -.015]), with older age predicting poorer lure discriminability as expected. The effect of age on MMN was significant, $B = -.009$, $SE = .002$, $p < .001$, 95% CI [-.013, -.005], as well as the effect of MMN on lure discrimination, $B = .620$, $SE = .230$, $p = .007$, 95% CI [.174, 1.080]. Critically, the indirect effect of age on lure discriminability through MMN amplitude as a reached significance, $B = -.005$, $SE = .003$, $p = .019$, 95% CI [-.012, -.002], thereby showing partial mediation. This indirect effect accounted for 19.49% of the variance from the total effect of age on lure discriminability.

As for foil discrimination, results showed that a significant direct effect of age on discriminability (*B* = -.038, *SE* = .006, *p* < .001, 95% CI [-.048, -.026]); as expected, older age was predictive of poorer foil discriminability. The effect of MMN on foil discrimination (*B* = -.155, *SE* = .375, *p* = .680, 95% CI [-.786, .381]) as well as the indirect effect (*B* = .001, *SE* = .003, *p* = .681, 95% CI [-.004, .007]) were both non-significant. The same pattern of results was found for this mediation model when replicating this analysis without five older adults who endorsed all 10 foil probes as "old". In summary, results show that MMN amplitude significantly mediated the predictive relationship of age on lure discriminability, but was not a significant mediator for age on foil discriminability.

Discussion

The present study aimed to examine the extent to which the MMN, as a measure of incidental encoding within sensory memory, accounts for differences in mnemonic discrimination in aging. The MMN was generated using a passive oddball paradigm with standard and deviant tone sequences; memory for these target stimuli were subsequently tested against similar lures and dissimilar foils. Across the entire sample, correlation matrices showed that age, MMN amplitude, and memory performance were each significantly correlated with one another. Consistent with prior research, we found that older adults showed attenuated MMN amplitudes relative to young adults. This finding was also coupled with worse target-lure and target-foil discriminability. We extend analyses reported in Herman et al. (2023) with regression models showing that the MMN predicted lure discriminability over and above age. Critically, MMN amplitude partially mediated the relationship between older age and declines in lure discrimination, but not foil discrimination. Given that the MMN selectively accounted for mnemonic discrimination performance rather than episodic memory *per se*, findings demonstrate

the sensitivity of the MMN to auditory pattern separation integrity in aging. These findings indicate that age differences in incidental encoding may be a potential mechanism in explaining age-related declines in mnemonic discrimination.

Sensitivity of the MMN to Auditory Pattern Separation

Studies using behavioural measures (Davidson et al., 2019; Gellersen et al., 2021), fMRI (Bowman et al., 2019; Koen, 2022; Zheng et al., 2018), and EEG (Lee et al., 2022; Sommer et al., 2019) have all shown age-related perceptual changes at encoding in service of successful retrieval. However, this research has been mainly restricted to associative learning in the visual domain. The present thesis extends this literature to perceptual influences on subsequent memory in an incidental, non-attentive context and to the auditory domain. Our correlation analyses show that the MMN amplitude relates to performance in both lure and foil discrimination. Interestingly, this contrasts with data reported from the same sample of young adults in Herman et al. (2023), where MMN amplitude was only correlated with performance in lure discrimination, and not foil discrimination. As young adults showed clear ceiling effects in both hit rates for targets and foils, we speculate that these data lacked variability to detect a substantial association between MMN and foil discrimination (but nonetheless still captured performance representative of "old-new" recognition memory performance in healthy adults). Therefore, the inclusion of data from older adults in the present study better clarified this relationship across the lifespan by capturing greater variability in target and foil endorsement in older age.

To disentangle associations between the MMN, age, and memory performance, regression and mediation models were conducted, showing that MMN amplitude predicted lure discrimination performance above and beyond the predictive value of age. In other words, the MMN, as a marker of individual differences in incidental encoding, uniquely predicted

subsequent mnemonic discrimination performance—and, in addition, mediated the relationship between older age and worse mnemonic discrimination performance. This finding contrasted with results for foil discrimination, in which performance here was better explained by the effects of age than differences in MMN amplitude. Findings point to the MMN as index of encoding that predicts subsequent lure discrimination—and by proxy, integrity of the pattern separation process given its relevance to encoding. Other research has also suggested that violations of sequential predictions bias hippocampal states towards encoding of novel information, thereby promoting pattern separation (Bein, Duncan, et al., 2020). Similarly, in the present study, violations of stimulus regularity manifested by the MMN may have promoted hippocampal encoding of auditory information and resistance to interference from lure sequences. Indeed, the integrity of the dentate gyrus (DG), a hippocampal region necessary for pattern separation (Baker et al., 2016; Wang et al., 2023; Yassa et al., 2011), deteriorates in aging compared to other hippocampal regions. Additional evidence points to decreased DG volume and DG hyperactivity associated with mnemonic discrimination deficits in aging (Dillon et al., 2017; Yassa et al., 2011). Notably, our findings are also consistent with mediation analyses with a combined sample of healthy older adults and older adults with mild cognitive impairment (MCI, Dillon et al., 2017). These authors show DG integrity (as measured by fractional volume via diffusion tensor imaging) significantly mediated the relationship between age and mnemonic discrimination performance in the visual domain. In sum, the present results show that the MMN can be sensitive to the integrity of hippocampally-mediated processes, particularly pattern separation.

Our findings linking the MMN to subsequent memory also add to prior literature on the role of the hippocampus for detecting novelty (Knight, 1996; Köhler et al., 2005) as well as

associative mismatch—when there is a discrepancy between the stimulus predicted to appear next in a sequence versus the actual stimulus presented. Several fMRI studies have specifically implicated the hippocampal CA1 subfield in associative mismatch detection (Chen et al., 2011; Duncan et al., 2009, 2012; Kumaran & Maguire, 2006, 2007; Long et al., 2016), which has been further investigated using magnetoencephalography (MEG; Garrido et al., 2015; Recasens et al., 2018). Here, participants performed a distractor working memory task while exposed to learned sequences of visual objects. In these efforts, greater hippocampal CA1 activity was found when the latter half of the sequence switched order and violated top-down expectations. Interestingly, this research has yet to be investigated in tandem with MMN measurement, aside from Recasens et al. (2018). In this study, MEG was recorded while participants in each trial were presented a 2.1s-long, unique four-tone sound sequence, after which the same sequence was repeated (predictable sequences) or repeated with the third and fourth tones switched in order (mismatch sequences). Throughout the paradigm, participants completed a distractor one-back working memory task. When comparing mismatch to predictable sequences, the authors indicated the presence of the magnetic MMN counterpart at the onset of both the third and fourth position of the sequence, which were detected at the right Heschl's gyrus, superior temporal gyrus, and ventromedial prefrontal cortex (vmPFC). The presence of these two MMN-like responses was accompanied by changes in functional connectivity between the right hippocampus and vmPFC (as measured via Granger causality) spanning theta and alpha frequency bands. This finding is in line with similar research using MEG in the visual domain, finding that effective connectivity in the theta band from vmPFC to hippocampus was associated with mismatch detection (Garrido et al., 2015). However, whether these hippocampal mismatch responses truly reflect the same construct captured by the MMN is unclear. Such paradigms employed by Recasens and

colleagues (2018) and others (Bein, Duncan, et al., 2020; Duncan et al., 2009; Hannula & Ranganath, 2008; Kumaran & Maguire, 2006) mimic a delayed match-to-sample task rather than presenting stimulus regularity with a common standard stimulus. Furthermore, the distractor task employed by this research involved a working memory component and effortful attention to stimulus changes rather than incidental learning.

The key distinction between these two bodies of literature may therefore rest in differential roles of prediction. The role of the hippocampus in detecting associative mismatch may be limited to violations of associative learning requiring attention, such as mismatched stimulus pairs or changes in object relationships within a learned sequence (for example, "mismatch" changes in the layout of furniture in a learned, familiar room described by Duncan and colleagues (2012)). These errors in prediction contrast with those generated from the MMN, which originate from changes within auditory sensory memory in the absence of associative learning or conscious attention (Bader et al., 2021; Coy et al., 2021; Näätänen et al., 2007; Sussman et al., 2014). Indeed, research has yet to show a difference in MMN amplitude or scalp topography in individuals with hippocampal lesions compared to controls (Alain, Woods, et al., 1998). Further, although the MMN response involves bilateral temporal sources, the hippocampus has yet to be identified as a putative generator (Cooray et al., 2014; Garrido, Kilner, Kiebel, et al., 2009). Given this research, the MMN from the present study may therefore mediate age-related deficits in pattern separation via changes in connectivity among extrahippocampal regions, such as with prefrontal regions that deteriorate in aging (Campbell et al., 2020; Lustig et al., 2007; see Amer & Davachi, 2023 for review). The exact role ascribed to the hippocampus in sensory memory continues to be investigated.

Implications for the MMN

Much research has shown and confirmed smaller MMN amplitudes in older than young adults, suggesting age-related deficits in central auditory processing and perceptual discrimination in aging (Alain & Woods, 1999; Cheng et al., 2013). Our findings are consistent with this literature, extending age-related attenuations in the MMN to abstract, higher-order regularity violations such as early violations in pitch contour. However, little research has examined the mechanisms underlying these age-related changes in the MMN. This literature has suggested either age-related deficits in the encoding of auditory stimuli within sensory memory (which may involve greater contributions from temporal areas) or violations of top-down expectations (which may involve greater contributions from frontal areas, Fitzgerald & Todd, 2020; Garrido, Kilner, Stephan, et al., 2009). Future research may decompose the MMN recorded from sensor space into discrete sources to clarify the extent of its frontal and temporal components in mediating its relationship with subsequent memory. Indeed, dynamic causal modelling (a method of decomposing time series data into a network of discrete sources for functional connectivity, Friston et al., 2003) has quantified a hierarchical network of distributed cortical sources that best accounts for automatic change detection in oddball paradigms. This research has proposed a five-node cortical network that best explains the underlying sources of the auditory MMN, specifically bilateral primary auditory areas, bilateral superior temporal gyri, and the right inferior frontal gyrus (Garrido, Kilner, Kiebel, et al., 2009). This has also been demonstrated using fMRI (Doeller et al., 2003; Opitz et al., 2002). Future research may investigate how frontal and temporal source activity underlying the MMN changes in aging and relates to episodic memory.

Few studies have investigated brain-behaviour relationships concerning the MMN. Not surprisingly, greater MMN amplitude has been shown to account for better perceptual

discrimination between stimuli (Aaltonen et al., 1994; Pakarinen et al., 2007). Studies have further shown associations between the MMN and performance on neuropsychological tests. For young adults, greater MMN amplitude has been shown to be correlated with greater performance in spatial working memory (Bonetti et al., 2018) and visuospatial reasoning (Beauchamp & Stelmack, 2006; De Pascalis et al., 2014). Within healthy older adults, Kisley et al. (2005) demonstrated that greater MMN amplitude (measured by a single frontal midline electrode) was correlated with better performance on tests of auditory verbal learning/memory, motor planning, and inhibition. These findings were replicated in a sample of healthy older adults and older adults with mild memory difficulties and while controlling for age, sex, and hearing loss (Foster et al., 2013). However, the basis for these correlations remains unclear, as these findings show a relationship between MMN amplitude measured in one paradigm, but behavioural performance measured on a separate paradigm that is typically in a different sensory modality (e.g., auditory MMN with a visual behavioural paradigm). Furthermore, these findings may be attributed to age-related differences in prefrontal functioning or concurrent perceptual declines in auditory and visual domains (Alain et al., 2021; Lindenberger & Ghisletta, 2009). Our study therefore extends this literature in examining relationships between the MMN and elements of higher cognition (i.e., long-term episodic memory) within the *same* paradigm—by testing for recognition performance for the same stimuli used to generate the MMN. By constraining both encoding and retrieval stages to the same sensory modality and paradigm, we reinforce that individual differences in MMN can index neural representations of incidental encoding of stimuli, which, in turn, can account for individual differences at later retrieval.

The use of standard and deviant auditory pure-tone sequences to elicit the MMN has been employed by many other studies (Alain et al., 1998, 1999; Fujioka et al., 2004; Tervaniemi et al.,

2001, 2006; Trainor et al., 2002; see Paavilainen, 2013 for review). These higher-order violations in pitch contour differ from the conventional oddball paradigm involving frequency deviants of simple pure tones (Näätänen et al., 2012). Our oddball paradigm was designed to elicit the MMN via higher-order pitch contour violations of auditory stimuli in service of studying its relationship with episodic memory, as the traditional MMN recorded by frequency deviants from simple pure tones is unlikely to be feasible for this aim. The use of complex auditory sequences also allowed for the measurement of mnemonic discrimination of lures separate from the general "old-new" effect in episodic memory generated by foils. However, given that the onset of the MMN occurred before the offset of the tone sequence stimulus, it can be argued that the MMN elicited in the present study may arise from early frequency violations from the first few tones rather than generated by violations from the entire auditory tone sequence. The use of three-tone sequences may have been sufficient in both eliciting the MMN and measurement of mnemonic discrimination.

Other recent work has also used standard and deviant tone sequences to investigate prediction error and perceptual discrimination at the behavioural level (Bader et al., 2017, 2021; Coy et al., 2021). These studies have mainly relied on active oddball paradigms (i.e., requiring participants to respond to deviance detection), as opposed to passive oddball paradigms which elicit the MMN without requiring a behavioural response. Therefore, in the present study, a passive oddball paradigm was chosen to examine how incidental encoding relates to subsequent precision in memory all while minimizing the influences of attention.

Given that the MMN can also be elicited with visual stimuli (Pazo-Alvarez et al., 2003), future research may explore perceptual contributions to mnemonic discrimination in the visual domain. Results may also inform clinical deficits in the interplay between perception and

memory (Näätänen, 2003), as changes in MMN amplitude and concurrent declines in episodic memory are present in clinical populations such as those with amnestic MCI (Lindín et al., 2013), Alzheimer's disease (Jiang et al., 2017), and schizophrenia (Baldeweg et al., 2004).

Implications for Mnemonic Discrimination in Aging

As expected, we found that older adults showed worse lure discriminability and foil discriminability on the APST than young adults. For each group, lures were more often incorrectly endorsed as "old" compared to either target or foils. Although young adults consistently showed ceiling performance for endorsing foils as "new," foil endorsement rates were more variable for the older adult sample, contrary to expectations. As many as three older adults scored all ten presentations of the foil probes in the retrieval phase as "old" (but did not substantially influence the pattern of results). Greater variability in foil hit rates may be explained by more cautious, conservative strategies employed by older adults, as demonstrated by age-related speed-accuracy trade-offs in many other cognitive tasks (Forstmann et al., 2011; Salthouse, 1979). Older adults may have been more likely to endorse novel foil items as old if they were convinced the foil had been played only once or twice amongst the tone sequences in the 25-minute exposure phase. Furthermore, this variability may also be driven by presenting the probes a total of 10 repetitions per stimulus type. Given that there was only one foil stimulus type in the APST, repetitive probing may have biased older adults to be more familiar with the foil sequence over the course of the test phase. Moreover, since the foil sequence was distinctly pitched down compared to standards and deviants, older adults may have had less discrete representations of these lower-pitched stimuli in memory, thereby misattributing foil probes as being presented in the encoding phase rather than the test phase.

Although age-related declines in mnemonic discrimination has been extensively studied in the visual domain (Davidson et al., 2019; Ly et al., 2013; Stark et al., 2013, 2015; Stark & Stark, 2017; Yassa et al., 2010, 2011), this has yet to be systematically studied in the auditory domain. It should be noted that, although the MST is a widely-used paradigm to study aging and visual mnemonic discrimination (Stark et al., 2013), the APST was not designed to be a pure auditory analog. The MST tests memory from a library of everyday objects, whereas the APST tests memory for the same two abstract, auditory tone sequences. A true auditory analog of the MST would incorporate everyday sounds (i.e., vacuum cleaner, alarm clock, bells), a version of this paradigm has undergone preliminary testing (Khurram, 2022; Wang et al., 2023). The measurement of auditory mnemonic discrimination may be particularly tricky to capture given that sounds do not occur in isolation, and vary in multiple aspects of acoustics even over very short time intervals. Ideally, acoustic stimuli should be matched in frequency, time, complexity, and salience. To this end, targets and lures on the APST comprised the same five tones but in a different temporal arrangement. The design of the APST therefore favours internal validity over generalizability by using novel, pre-experimentally unfamiliar stimuli, given that familiarity of stimuli promotes pattern separation (Bein, Reggev, et al., 2020). The use of abstract, atonal auditory stimuli lacking in semantic content in the current paradigm also serves to maximize age-related differences given older adults' greater reliance on familiarity and schemas compared to young adults (Anderson et al., 2019). The present findings thus provide a first step in examining behavioural pattern separation in the auditory domain in a controlled, laboratory setting.

Late Discriminative Negativity

Both young and older adult groups also showed an LDN component in addition to the MMN during the passive oddball phase, occurring at a time window coinciding with the offset of

the stimulus. This finding of both an MMN and LDN is consistent with an oddball study using tone pairs with violations in pitch contour (Zachau et al., 2005). Compared to the MMN, the LDN has received scant attention. Few studies have characterized the LDN in proposing this ERP as an endogenous response to change detection that consistently occurs after offset of auditory stimuli. For instance, the LDN has been elicited in research examining speech perception in language development in infants and young children using EEG (Cheour et al., 2001; Martynova et al., 2003) and MEG (Huotilainen et al., 2003). Although one study attributed the LDN to greater transfer of sensory memory into long-term memory (Peter et al., 2012), empirical evidence for this interpretation is lacking, and no study so far has demonstrated how its functional significance differs from that of the MMN.

Our findings of the LDN, with its late latency occurring after stimulus offset, may index global gestalt violations in pitch contour. Therefore the functional significance of the LDN may relate to pattern completion—a hippocampal process by which incomplete or degraded sensory cues are generalized to support holistic retrieval (Rolls, 2013, 2016). This may be especially relevant to understanding memory in aging, given that aging is associated with biases in favour of pattern completion and away from pattern separation (Ly et al., 2013; Reagh et al., 2014; Vieweg et al., 2015; Wynn et al., 2021). However, our exploratory correlations failed to show evidence for associations between LDN amplitude with either age or subsequent memory performance. How LDN relates to pattern completion, or whether higher-order abstract violations consistently elicit a clear double dissociation of ERPs, are open questions for future research.

Limitations

Some methodological limitations should be considered in interpreting results. First, participants aged 35 to 54 years of age were not represented in the sample. Thus, it is inferred that MMN amplitudes and mnemonic discrimination performance for these middle-aged participants are intermediate between young and older adults. Future studies with this dataset that specifically target this population are encouraged.

Next, the APST tests for mnemonic discrimination in a controlled manner at the expense of ecology validity. A complementary paradigm taxing auditory pattern separation may use everyday sounds, soundscapes, or verbal stimuli. Furthermore, the inherent nature of the oddball paradigm necessities one stimulus type (standard) to be presented more than another (deviant). To mitigate this, the oddball paradigm implemented a low standard to deviant ratio of seven to three, and the deviant stimulus was presented a total of 300 times to ensure adequate transfer of the deviant stimulus from sensory memory into long-term memory. Exploratory analyses within young adults as reported in Herman et al. (2023) also confirmed no difference in endorsement rates between standard and deviant targets, or between the three lure types. Nevertheless, the use of a roving MMN paradigm (Garrido et al., 2008; Haenschel et al., 2005) may mitigate these effects on subsequent memory. In this paradigm, both standard and deviant stimuli switch roles so that each stimulus type is presented equally. This paradigm would ensure the MMN response is elicited solely due to violations of higher-order regularities in a process pure manner without contaminations from frequency-specific differences between stimuli.

Finally, not all older adults in the present sample scored above the cut-off of 26/30 for the MoCA, a brief screening measure sensitive to MCI. Despite this, only a minority of older adults in the sample scored slightly below the cut-off, which further allowed better generalizability of findings and helped to ensure adequate variability in both neural and behavioural findings. Some

research has suggested that this cut-off is too stringent for healthy aging (Carson et al., 2018), even for highly educated older adults (Elkana et al., 2020). The present study therefore employed further neuropsychological testing with our older adult participants to verify that episodic memory performance (and other cognitive abilities) were within an expected range for participants' age.

Conclusion

The present study aimed to clarify how age differences at encoding can account for declines in mnemonic discrimination in the auditory domain. Results demonstrate that the MMN can serve as an index of incidental encoding given its automatic capture of change detection, and can be used to examine how perception influences subsequent memory while minimizing the influences of attention. We show that age-related declines in auditory mnemonic discrimination can be accounted for by deficits in encoding processes. Findings also reinforce the sensitivity of the MMN to changes in pattern separation integrity that accompany healthy aging. Given the vast literature showing concurrent declines in episodic memory and aberrations in MMN amplitude in clinical populations, this ERP shows new promise in transcending its role in sensory memory and informing encoding processes in service of higher-order cognition.

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Tables

Table 1

Participant Demographics and Neuropsychological Data

Variable	Young Adult Means (SD) *n=30*	Older Adult Means (SD) *n=33*	
		Raw	Scaled
Demographics			--
Age (years)	22.51 (3.59)	69.09 (8.36)	--
Education (years)	15.19 (2.07)	16.58 (2.14)	--
Sex (F:M)	12:18	14:19	--
TICS-m	--	37.21 (3.76)	--
MoCA	--	26.76 (2.02)	--
Estimates of IQ			
WASI Matrix Reasoning		27.46 (9.65)	14.42 (1.86)
WASI Vocabulary		63.63 (8.52)	11.88 (2.42)
Memory			
CVLT-II Total Learning	--	46.92 (12.50)	11.75 (3.60)
CVLT-II Short Delay FR	--	10.17 (3.51)	11.71 (4.42)
CVLT-II Long Delay FR	--	10.25 (3.52)	11.39 (3.82)
CVLT-II Recognition		2.85 (0.76)	10.54 (3.02)
WAIS-III Digit Symbol IL PR	--	12.54 (4.43)	10.29 (1.23)
WAIS-III Digit Symbol IL FR	--	7.25 (1.07)	10.33 (1.01)
Executive Functioning and Processing Speed			
WAIS-III Digit Symbol Coding	--	66.04 (13.37)	13.38 (2.65)
WAIS-IV Digit Span Forward		10.67 (2.20)	11.38 (2.86)
WAIS-IV Digit Span Backward		9.79 (1.77)	12.58 (2.22)
WAIS-IV Digit Span Sequencing		9.25 (2.40)	12.63 (2.93)
D-KEFS Letter Fluency	--	49.50 (12.71)	14.25 (3.45)
D-KEFS Category Fluency	--	43.13 (6.50)	13.83 (2.58)
D-KEFS Category Switching	--	14.29 (3.13)	12.71 (3.70)
Trail-Making Test A	--	25.67 (7.56)	14.08 (2.78)
Trail-Making Test B	--	67.21 (27.61)	13.29 (2.84)
Questionnaires			
GAD-7	--	1.38 (1.93)	--
PHQ-8	--	1.88 (2.46)	--

Note. Neuropsychological tests of intelligence, memory, executive functioning, and processing speed were administered with a subset of older adults above 60 years of age (*n* = 24). TICS-m = modified Telephone Interview of Cognitive Status (raw score out of 50); MoCA = Montreal Cognitive Assessment; WASI = Wechsler Abbreviated Scale of Intelligence; WAIS = Wechsler Adult Intelligence Scale; CVLT = California Verbal Learning Test; IL= Incidental Learning; FR = Free Recall; PR = Paired Recall; D-KEFS = Delis Kaplan Executive Functioning System; GAD-7 = Generalized Anxiety Disorder 7-item Scale; PHQ-8 = Patient Health Questionnaire 8-item Scale.

Table 2

Mnemonic Similarity Task (MST): Older Adult Hit Rates

Response	Target	Lure	Foil
Old	.78 (.18)	.44 (.17)	.08 (.08)
Similar	.11 (.11)	.28 (.18)	.15 (.14)
New	.11 (.12)	.17 (.10)	.78 (.15)

Note. Proportion endorsed for each stimulus and response type on the MST. Data are in means (SDs). Hit rates for the young adult group are reported in Herman (2023).

Table 3

Auditory Pattern Separation Task (APST): Discrimination Phase Hit Rates

Condition	Young Adults *n=30*	Older Adults *n=33*
Overall	.965 (.046)	.844 (.119)
Repeated Pairs	.978 (.076)	.963 (.076)
Different Pairs	.959 (.054)	.796 (.153)

Note. Hit rates for correctly discriminating stimulus pairs in the discrimination phase of the APST. Data are in means (SDs).

Table 4

Summary of Cluster-Based Statistics: Young Adult Standard vs. Deviant Waveforms

Electrode Cluster		Time (ms)	*p*-value
1	FP1, AF7, AF3, F1, F3, F5, FC5, FC3, FC1, C1, C3, C5, T7, TP7, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, TP8, CP4, CP2, P8, P10, PO8, O2, CB1, CB2, TP9, TP10	162-381	<.001
2	FP1, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, T7, TP7, CP5, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C6, T8, TP8, CP6, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10, FT9, FT10, F9, F10, LO1, LO2, IO1, IO2	158-385	<.001
3	FP1, AF7, AF3, F1, F3, F5, FC5, FC3, FC1, C1, C3, CPz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FC4, FC2, FCz, Cz, C2, C4	516-658	<.001
4	T7, TP7, CP5, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, FT8, C6, T8, TP8, CP6, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10, FT10, F10	531-659	<.001
5	AF3, F1, F3, FC3, FC1, C1, C3, C5, T7, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, POz, Pz, CPz, AF4, AFz, Fz, F2, F4, F6, FC6, FC4, FC2, FCz, Cz, C2, C4, CP4, CP2, P2, P4, P6, PO4	385-525	<.001
6	FP1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, T7, TP7, P5, P7, P9, PO7, O1, Iz, Oz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, C6, T8, TP8, CP6, P8, P10, PO8, O2, CB1, CB2, TP9, TP10, FT9, FT10, F9, LO1, LO2, IO2	387-525	<.001

Table 5

Summary of Cluster-Based Statistics: Older Adult Standard vs. Deviant Waveforms

Electrode Cluster		Time (ms)	*p*-value
1	FP1, AF7, AF3, F1, F3, F5, FC5, FC3, FC1, C1, C3, TP7, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, CPz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FC6, FC4, FC2, FCz, Cz, C2, C4, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10	137–408	<.001
2	FP1, AF7, AF3, F1, F3, F5, F7, FC5, FC3, FC1, C1, C5, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, C2, C4, C6, F9, LO1, IO1	527–682	<.001
3	C5, TP7, CP5, CP3, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, Pz, FT8, FC6, C4, C6, T8, TP8, CP6, CP4, CP2, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP10	506–686	<.001
4	FP1, AF7, AF3, F1, F7, FT7, FC3, FC1, C5, T7, TP7, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C4, C6, T8, TP8, CP6, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10, FT9, FT10, F9, F10, LO1, LO2, IO1	291–465	<.001
5	FP1, AF7, AF3, F1, F3, F5, F7, FC5, FC3, FC1, C1, C3, C5, CP3, CP1, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FT8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, LO1, LO2, IO1, IO2	145–207	<.001
6	F3, FC5, FC3, C3, C5, CP5, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10	418–484	.010

Table 6

Summary of Cluster-Based Statistics: Young vs. Older Adult Difference Waveforms

Electrode Cluster		Time (ms)	*p*-value
1	FP1, AF7, AF3, F1, F3, F5, F7, FT7, FC5, FC3, FC1, C1, C3, CP1, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, FC6, FC4, FC2, FCz, Cz	266–355	<.001
2	TP7, P1, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, F8, FT8, C6, T8, TP8, CP6, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10, FT10, F10, LO2, IO2	270–371	.016
3	FP1, AF7, AF3, F1, F3, F5, FC5, FC3, FC1, FPz, FP2, AF8, AF4, AFz, Fz, F2, F4, F6, F8, FC6, FC4, FC2, FCz, Cz, C2, C4, C6, CP2	190-–56	.019
4	T7, TP7, CP5, CP3, P1, P3, P5, P7, P9, PO7, PO3, O1, Iz, Oz, POz, T8, TP8, P2, P4, P6, P8, P10, PO8, PO4, O2, CB1, CB2, TP9, TP10	190–258	.029
5	AF3, F1, F3, FC3, FC1, C1, C3, CP5, CP3, CP1, P1, P3, P5, P7, P9, PO7, PO3, O1, POz, Pz, CPz, AF4, AFz, Fz, F2, F4, FC4, FC2, FCz, Cz, C2, C4, CP4, CP2, P2, PO8, PO4, CB1	369–504	.037

Table 7

Correlation Matrix Between Age, MMN, LDN, and Discriminability

Variable	Age	MMN	LDN	d' (T-L)	d' (T-F)
Age	-				
MMN	-.515***	-			
LDN	-.029	.427***	-		
d' (T-L)	-.702***	.558***	.046	-	
d' (T-F)	-.644***	.298*	-.094	.546***	-

*$p < .05$. **$p < .01$. *** $p < .001$.

Note. Data are correlation coefficients. Values for MMN are reversed in sign, such that a positive coefficient denotes increases in MMN amplitude correlated with increases on another variable. d'(T-L) = d-prime for target-lure discriminability. d'(T-F) = d-prime for target-foil discriminability.

Table 8

Regression Results: Age and MMN on Target-Lure Discriminability

Model	Variable	B	SE	BCa CI [LL, UU]	β	*p*
1	MMN	1.293	.242	[.829, 1.802]	.588	<.001
2	MMN	.620	.235	[.187, 1.080]	.268	.011
	Age	-.022	.004	[-.030, -.014]	-.564	<.001

Note. Values for MMN are reversed in sign, such that a positive coefficient denotes greater MMN amplitude predictive of greater d-prime values. Results were obtained through 1000 bootstraps. BCa CI = bias-corrected accelerated 95% confidence interval obtained through 5000 bootstraps; LL = lower limit; UL = upper limit.

Table 9

Regression Results: Age and MMN on Target-Foil Discriminability

Model	Variable	B	SE	BCa CI [LL, UU]	β	*p*
1	MMN	.993	.318	[.336, 1.578]	.298	.018
2	MMN	-.155	.286	[-.786, .356]	-.046	.590
	Age	-.038	.006	[-.049, -.027]	-.667	<.001

Note. Values for MMN are reversed in sign, such that a positive coefficient denotes greater MMN amplitude predictive of greater d-prime values. Results were obtained through 1000 bootstraps. BCa CI = bias-corrected accelerated 95% confidence interval; obtained through 5000 boostraps; LL = lower limit; UL = upper limit.

Figure Captions

Figure 1. Frequency distribution and temporal arrangement of five 100-ms tones comprising each stimulus type.

Figure 2. Schematic illustration of the three phases comprising the Auditory Pattern Separation Task (APST).

Figure 3. Grand-averaged frontal-central midline (FCz) ERPs for A) young adults and B) older adults elicited by standard and deviant trials, and the resulting difference waveform. The mismatch negativity (MMN) and the late discriminative negativity (LDN) identified. Zero ms denotes stimulus onset.

Figure 4: Sample waveforms for a A) young adult and B) older adult participant across a cluster of seven frontal and frontocentral electrode sites (AFz, F1, Fz, F2, FC1, FCz, FC2). Waveforms in black are standard trials; waveforms in red are deviant trials.

Figure 5. Raincloud plots and boxplots of Lure Discrimination Index (LDI) and Traditional Recognition Scores (TRS) on the Mnemonic Similarity Task for each group.

Figure 6. Boxplots of hit rates on the APST, Test Phase by condition for A) young adults and B) older adults.

Figure 7. Scatterplots of the correlation between MMN amplitude and A) d-prime for target-lure discrimination and B) target-foil discrimination. MMN amplitude values were derived from a cluster of seven frontal and frontocentral electrodes from 200 to 400 ms post-stimulus onset.

Figure 8. Schematics of the simple mediation models of the MMN mediating the relationship between age and A) lure discrimination, and B) foil discrimination. The MMN significantly

mediated age and lure discrimination, but not foil discrimination. Unstandardized path coefficients are reported. $^{**}p < .01$, $^{***}p < .001$

Figure 1

Schematic of the Auditory Pattern Separation Task

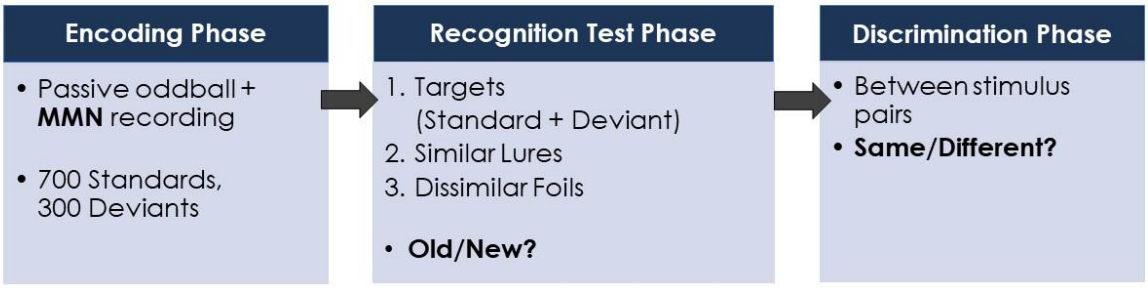
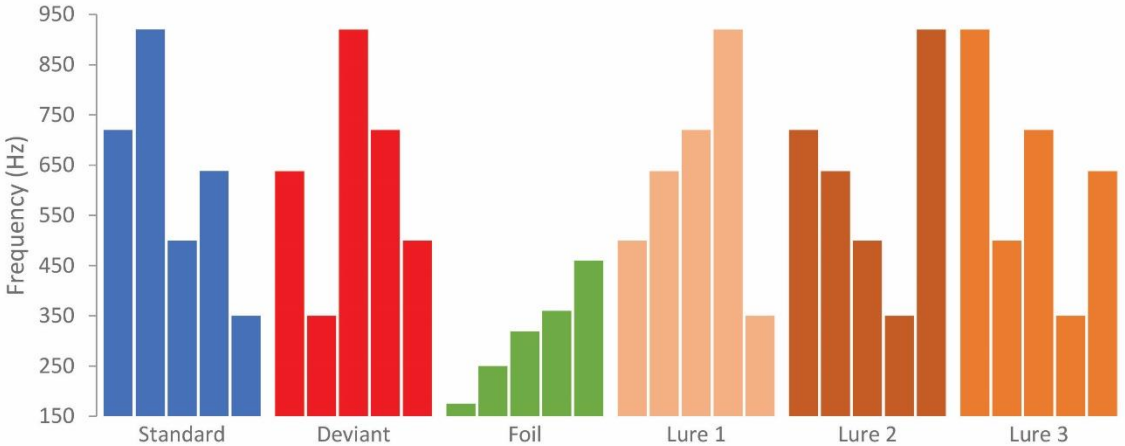


Figure 2

Frequency Distribution by Stimulus Type in the Auditory Pattern Separation Task



	Standard	Deviant	Foil	Lure 1	Lure 2	Lure 3
100 ms	720	638	175	500	720	920
200 ms	920	350	250	638	638	500
300 ms	500	920	319	720	500	720
400 ms	638	720	360	920	350	350
500 ms	350	500	460	350	920	638

Figure 3

Auditory Pattern Separation Task, Encoding Phase: Grand-Averaged Waveforms

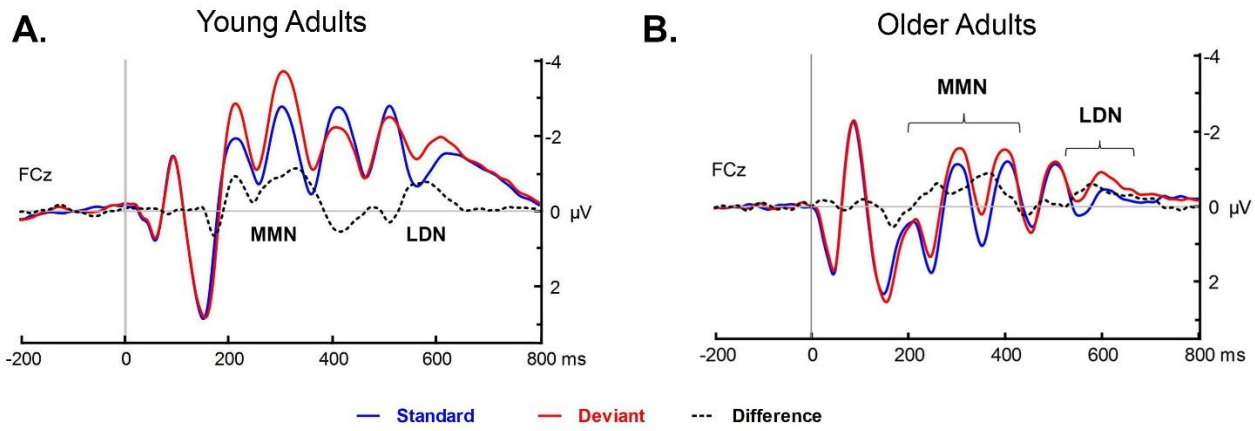


Figure 4

APST Encoding Phase: Sample Waveforms

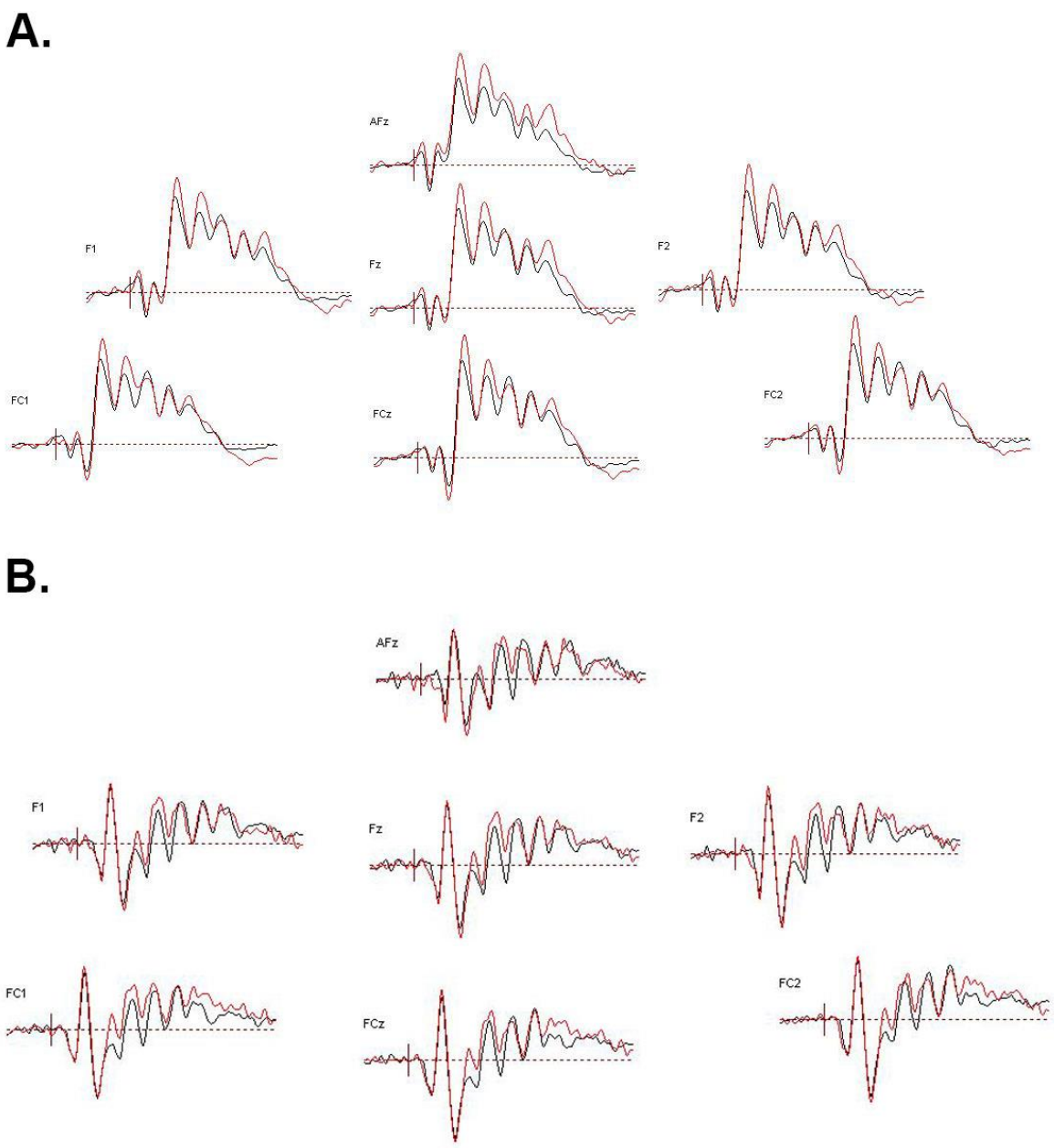


Figure 5

Mnemonic Similarity Task: Discriminability Performance per Group

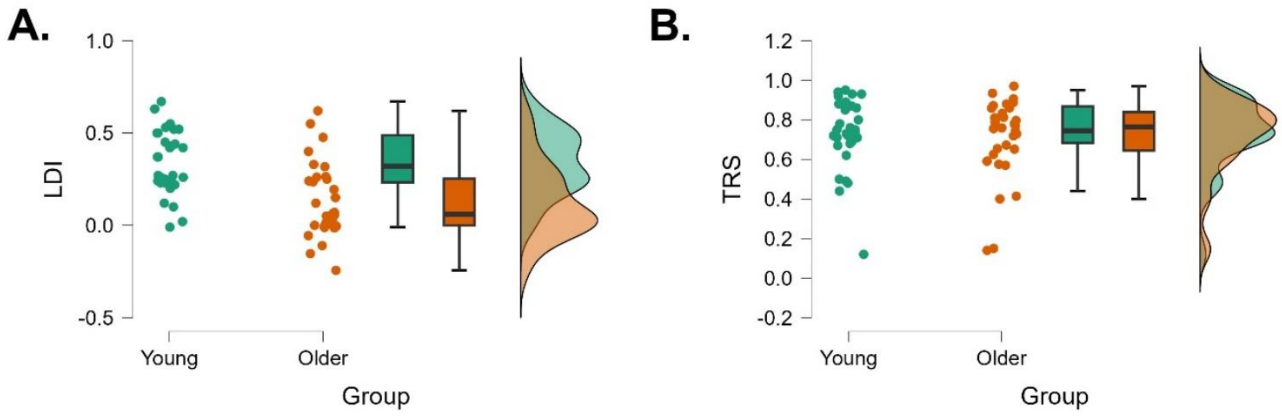


Figure 6

Auditory Pattern Separation Task, Recognition Phase: Box Plots of Hit Rates Per Group

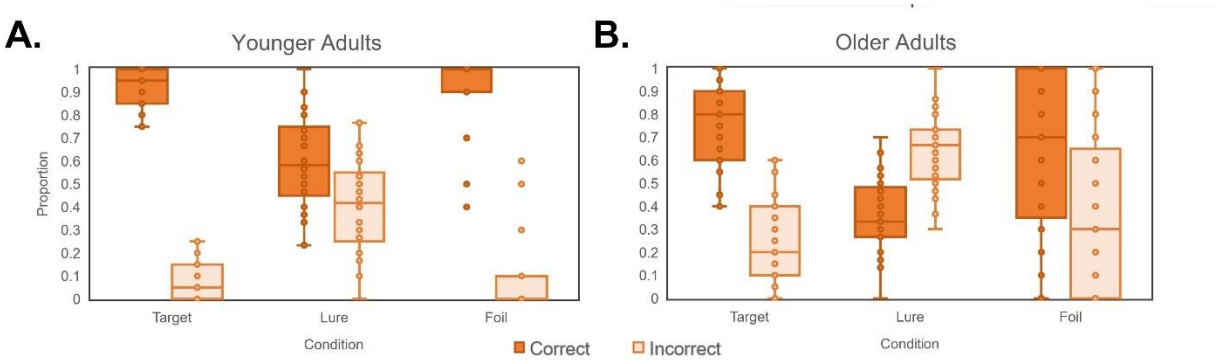


Figure 7

Relationship between MMN Amplitude and Recognition Performance

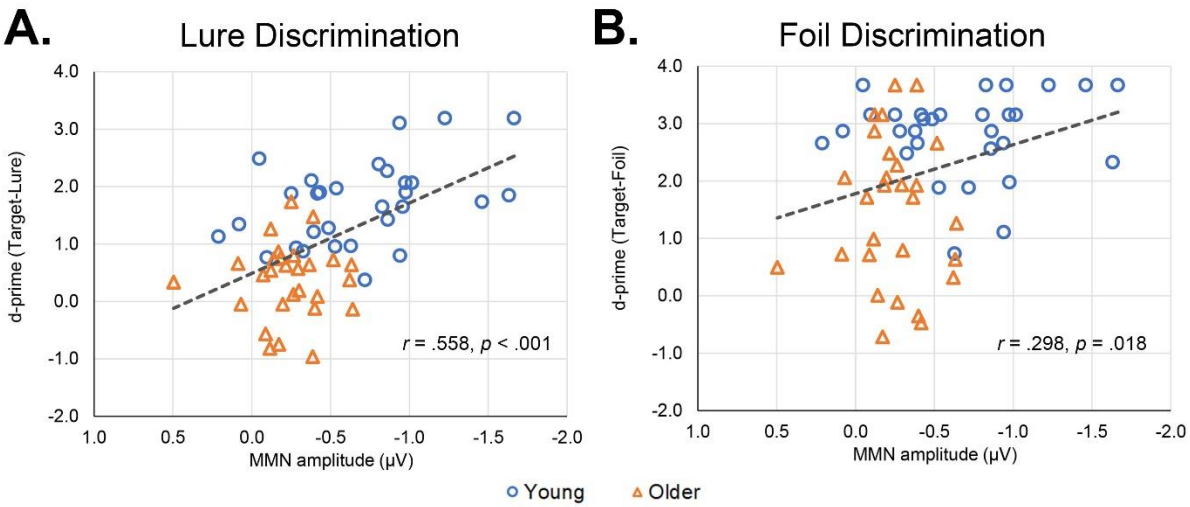


Figure 8

Schematic of Mediation Analyses for Age, MMN, and Discriminability