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Aging-related changes in auditory and visual integration measured with MEG

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Abstract

As noted in the aging literature, processing delays often occur in the central nervous system with increasing age, which is often attributable in part to demyelination. In addition, differential slowing between sensory systems has been shown to be most discrepant between visual (up to 20 ms) and auditory systems (< 5 ms). Therefore, we used MEG to measure the multisensory integration response in auditory association cortex in young and elderly participants to better understand the effects of aging on multisensory integration abilities. Results show a main effect for reaction times (RTs); the mean RTs of the elderly were significantly slower than the young. In addition, in the young we found significant facilitation of RTs to the multisensory stimuli relative to both unisensory stimuli, when comparing the cumulative distribution functions, which was not evident for the elderly. We also identified a significant interaction between age and condition in the superior temporal gyrus. In particular, the elderly had larger amplitude responses (~100 ms) to auditory stimuli relative to the young when auditory stimuli alone were presented, whereas the amplitude of responses to the multisensory stimuli was reduced in the elderly, relative to the young. This suppressed cortical multisensory integration response in the elderly, which corresponded with slower RTs and reduced RT facilitation effects in the elderly, has not been reported previously and may be related to poor cortical integration based on timing changes in unisensory processing in the elderly.

Keywords

Magnetoencephalography; auditory; visual; aging; multisensory integration

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Introduction

Multisensory integration has been well studied over the last decade. This has included both behavioral and neuroimaging studies to identify reaction time effects and the cortical areas associated with enhanced or suppressed responses to multisensory, relative to unisensory, stimuli. However, the question of how the aging brain responds to multisensory stimulation has been less well studied and the results generally provide a conflicting story of whether adults benefit from the redundant nature of multisensory stimuli or not [5,6,9,12,15]. Laurienti et al. [12] and Peiffer et al. [15] have suggested that these apparently conflicting results are likely due to the varied nature of the sensory and cognitive tasks themselves rather than other confounds.

Despite the growing literature about the effects of aging on multisensory integration, very few studies have been conducted using neuroimaging to identify the neurophysiological underpinnings of changes in multisensory integration with age [15]. We find MEG to be particularly well-suited for this task since it provides very good temporal resolution as well as good spatial resolution to understand the neural correlates (i.e., timing/amplitudes of cortical activations) associated with changes in RTs. Studies of multisensory integration have identified multiple cortical areas that are involved in this function such as primary and secondary sensory areas, in addition to the traditionally reported temporal/parietal association areas [4]. This study focuses on activity identified in superior temporal gyrus (STG), a location which includes the auditory association area, that is reliably activated across participants and has been shown to be intimately involved in auditory/visual integration [10,18,19].

Evoked potential studies have shown that timing in the brain changes with age (i.e., successive peaks in the waveforms are progressively longer in the elderly as information travels through the sensory system (e.g. [2,20])). Based on these reports, there also appears to be differential slowing between the sensory systems with a delay of up to 20 ms in the visual system compared to ~3-5 ms in the auditory system. Based on this differential slowing and known slowing in the brain, we hypothesized that the integration response, which has been identified in auditory association area, would be delayed or reduced in the elderly, relative to the young participants. We tested this hypothesis with realistic temporal delays for near and far sources in a perspective drawing of a soccer field. We expected the largest difference to occur with the near condition (peripheral visual condition) due to previously reported decrements in peripheral visual processing in the elderly [8,26].

Methods

Sixteen participants [8 young (20-33 years; 4 females) and 8 elderly (65-78 years; 5 females)] were run in an auditory/visual integration task using 3 stimulus conditions: auditory only (A), visual only (V) and combined auditory/visual (AV). Each participant provided written informed consent prior to study involvement (approved by Human Research Review Committee at UNM Health Sciences Center and NM VA R&D Committee) in accordance with the Declaration of Helsinki. The visual background in all conditions was a simplified soccer field with a net and goal tender; the outlines of the field provided linear perspective. Participants were instructed to maintain fixation on the goal tender (visual angle $0.54^\circ \times 0.81^\circ$). A soccer ball was presented in two locations in the lower visual field along the vertical meridian with the far stimulus (relative to the participant) in the central visual field (far: 0.32° at eccentricity of 0.54° below fixation) and the near stimulus in the parafoveal visual field (near: 0.8° at eccentricity of 3.8° below fixation). The size of the soccer ball was adjusted to be consistent with the cortical magnification factor (i.e., it was larger for the near condition) [17]. The auditory stimuli

were presented through ear tubes using etymotic transducers with a near/far manipulation of 6 db (1000 Hz tone; near: loud, far: quiet). The delay caused by the ~3m of auditory tubing (9 ms) was accounted for in the stimulus program. Since the stimuli were presented along the vertical meridian, there were no left/right differences in volume or time-of-arrival for auditory stimuli. In the AV near/far conditions A was delayed by 5/50 ms relative to V to simulate the known timing differences between realistic A and V stimuli, respectively. This delay simulates a near/far distance of 1.5/30 m from the participant. Participants were informed that the two modalities were never presented in a conflicting manner (e.g. one never heard a far tone with a near visual stimulus).

Due to the incompatibility of eye-tracker systems with MEG at the time of data collection, EOGs were used to monitor eye movements to indicate that participants were able to maintain fixation. Based on feedback during pilot testing, it was most efficient to maintain fixation, probably due to short ISIs (1.5 – 1.9 s) and unpredictable stimulus locations. In addition, onset latencies in primary visual cortex differed for foveal versus parafoveal locations as expected (no age effect: near = 91 ms, far = 112 ms, $F = 8.8$, $p < 0.005$, $df = 47$), see Stephen et al. [24], strongly suggesting that participants maintained fixation throughout the task.

In all conditions, participants were asked to respond as quickly and accurately as possible with a left/right index finger button press when stimuli were near or far, relative to themselves. Eight participants [4 young (2 female) and 4 elderly (2 female)] were run in a blocked version of this task; near and far conditions were randomized within the blocks (A, V, AV) and order of the blocks were randomized across participants. The other eight participants were run in a fully randomized version of the task, where all 6 conditions were presented in random order. Results were collapsed across the blocked and randomized designs since no significant differences were found between the two. The whole-head 122 channel Neuromag MEG data were acquired at 400 Hz sampling rate within a magnetically shielded room. Anatomical MRIs were obtained for each participant using a 1.5T Picker Edge MRI scanner to allow for registration of the dipole locations to anatomical locations. Standard head position information (fiducials and head shape) was obtained to co-register the MEG data measurements and source locations with respect to each individual's MRI using MRVIEW [16]. The fiducial points obtained using the Polhemus were matched to the fiducial points on the MRI with an automated coordinate transformation. The data were low-pass filtered at 50Hz and any large amplitude nonphysiologic noise was eliminated. In addition, any epochs with eye blinks that occurred in the window of interest (0-500 ms post-stimulus) were eliminated prior to signal averaging (~120 trials/condition).

Once the data were preprocessed and averaged, a calibrated-start, multi-dipole spatio-temporal modeling technique was used (see [16,25]) to determine the locations and timing of the sources contributing to the measured activity. The time interval, 30-300 ms post-stimulus, was analyzed to model the early responses. Once a proper model was obtained for each participant (i.e., determined by using a chi-squared goodness-of-fit measure), the individual source timecourses were characterized using a semi-automated peak characterization routine to obtain the peak amplitudes, latencies and durations (see [25] for details). This information was compiled across participants. Once consistent peaks were identified across participants, small time windows were used to capture peak amplitudes across individuals (45-55 ms, 90-100 ms) for statistical analyses. Direct comparisons of these mean peak amplitudes were performed using ANOVAs in a peak by age by condition design. Peak latencies for these two peaks were also compared across condition and age. The data were tested for outliers.

The behavioral data were analyzed by calculating the mean reaction time (RT) and percent correct in response to the near/far stimuli. Responses earlier than 100 ms or greater than 3 standard deviations from the individual subject mean were eliminated. In addition, the RTs were separated into quantiles (RTs are divided evenly where the median is the 0.5 quantile – see Fig. 1) and the cumulative probability function was calculated to better understand the distribution of the RTs across age and condition [13]. The predicted AV response is obtained by summing the unisensory quantiles and subtracting off the product of the unisensory quantiles. If the AV RT is significantly less than AV predicted for any quantile, then the additional facilitation cannot be explained by two independent inputs (i.e., it violates the statistical race model [13]). RTs were analyzed using 2-factor ANOVAs with age and condition as factors.

Results

No significant near/far differences were found in the behavioral RT results or in bilateral STG source timecourses. Therefore, the remaining results include the combined analysis of the near/far conditions. There was a main effect of age with RTs being slower in the elderly group compared to the young ($F(1,96) = 7.2$, $p = 0.009$ - see summary RTs in Table 1). There was a significant effect of condition with the post-hoc analyses showing that the RTs for the A condition were significantly longer than the RTs for the V and AV conditions ($F(2,96) = 5.1$, $p = 0.008$). There were no significant differences in percent correct across age or condition. There was no significant age by condition interaction ($F(2,96) = 0.1$, $p = 0.9$). The mean RTs and percent correct did not show evidence of multisensory facilitation, when compared with the fastest unisensory condition (i.e., RT(AV) was not distinguishable from RT(V)).

However, analysis of the RT quantiles showed a different pattern than the mean RTs (see Fig. 1). First, there was a significant difference in the AVpredicted minus AV quantiles with age as the factor. As expected, there was a significant main effect of quantile. To understand the age effect, we analyzed the quantiles separately by age. Similar to Miller et al [13], we performed t-tests at each quantile (accounting for multiple comparisons using standard Bonferroni correction) and found significant enhancement at the following quantiles for the young (0.2 – 0.95). We did not find significant facilitation at any of the quantiles for the elderly. RTs were generally faster for the elderly for the AV condition, but they did not reach significant levels. In sum, in addition to a general lengthening of RT with age, the young also showed AV facilitation across many RT quantiles whereas the elderly did not. This distinction was not evident when comparing mean RTs.

After performing source analysis for each participant and condition, we reliably found activity in bilateral superior temporal gyrus (STG), in the vicinity of primary auditory cortex, for conditions using auditory stimuli (A and AV conditions) as well as activity in occipital cortex for conditions using visual stimuli (V and AV conditions), as expected. Due to the close proximity of primary and secondary auditory areas, we assumed that the reported STG sources have contributions from both primary and auditory association areas [11]. A number of other cortical sources were localized across participants including superior temporal sulcus (STS), insular, lateral occipital, parietal, cingulate and supramarginal (SMG) cortices. As stated earlier, for the purpose of this paper we report on the results obtained in area STG, since multisensory integration effects have been reported for this region previously [10,18,19].

Similar to our previous studies [1,11,25], the timecourses from STG (left and right hemisphere STG sources were combined since there were no significant hemispheric differences) were compared across age category and condition with the average STG

timecourses presented for visualization purposes (see Fig. 2). The analysis of the STG timecourses focused on the first two peaks. The ANOVA showed a significant condition x peak x age category interaction ($F(1,200) = 3.8$, $p = 0.05$ – Fig. 2) explained in part by differences in overall responses in peak 1 versus peak 2. A main effect of age for peak 1 is evident with greater amplitude in the elderly across conditions (peak ~60 ms: $F(1,100) = 24.9$, $p < 0.0001$), similar to results in our previous aging studies [11,25]. In contrast, peak 2 reveals a significant interaction where elderly had larger amplitudes for A relative to AV, whereas the young had larger amplitudes for AV relative to A responses in area STG ($F(1,100) = 3.9$, $p = 0.05$). There was no significant difference in peak latency for peaks 1 or 2, which is also consistent with the averaged STG timecourses shown in Fig 2.

Similar analyses were performed for V and AV conditions for the occipital sources. A similar trend was identified, but the results were not significant.

Discussion

We identified RT facilitation for multisensory stimuli which violated the statistical race model in the young, but not in the elderly. Consistent with this finding we identified an interaction in the MEG measures showing that the AV response localized to STG is lower in amplitude in the elderly, relative to the young, but is preserved for the auditory alone condition. This is in contrast to the mean RT results which did not show significant facilitation for both auditory and visual conditions, as required for multisensory facilitation. This suggests that facilitation of cortical responses is more closely linked to quantile RT results rather than mean RT results. One advantage of the quantile RT analysis is that the raw RTs are normalized across participants such that it allows one to compare the pattern of the RTs across individuals. The pattern across most quantiles shows that facilitation is indeed seen in most trials for the young and is reflected in the enhancement in the STG timecourses. This suggests that variability in the raw RTs is likely influencing the lack of significance in the mean RTs in the young. The lack of significance in the quantile results for the elderly is also consistent with the lack of enhancement in the STG timecourse in the elderly group.

Contrary to our hypothesized near/far differences, no significant differences were found. This is likely related to our focus on area STG where the difference between auditory near/far conditions was a 6 dB change in volume. In a larger study focusing on auditory and visual regions, we expect to see near/far differences.

Our results are not consistent with some of the psychophysical results in the limited multisensory integration aging literature which suggest that the elderly receive more benefit from multisensory stimuli than the young [6,9,12,15]. Laurienti et al. [12] suggested that conflicting reports of both poorer and improved multisensory integration by older individuals are likely due to large differences in task designs. Stanford and Stein [22] argued that many of the multisensory studies have been designed specifically to obtain a facilitation in RTs. To obtain this enhancement the studies focused on presenting stimuli at or just above perceptual threshold. However, in many aspects of daily living, multisensory interactions are not at or near perceptual threshold. The current study was designed to optimize the electromagnetic response and did not present stimuli at or just above threshold detection. The results of Stanford et al. [21] suggest that many conditions in which the stimuli are not at or near threshold would not necessarily elicit enhancement but may show simple linear summation or even suppression. Diederich et al. (2009) raised the issue that more intense sensory stimuli may change the multisensory integration response in the elderly. If stimuli are close to threshold, the inverse effectiveness rule [23] may be enhanced in the elderly and lead to larger facilitation due to degradation in the peripheral sensory

modalities in the elderly relative to the young. However, if the stimuli are high contrast and the elderly can perceive the stimuli easily, this inverse effectiveness advantage may be lost. In addition, Colonius and Diederich (2004) proposed the TWIN model which says that the integration window is longer in the elderly, but due to peripheral timing changes, the probability of integration may be lower in the elderly. This may help explain the current results. In addition, Diederich et al. [7] updated their TWIN model suggesting that the probability of integration is lower in the elderly due to peripheral timing changes and more variability in the sensory timing. This is consistent with our current results showing poorer integration and may help explain the reduced amplitude AV response in STG in the elderly. While the elderly did show a trend for facilitation in the AV condition which may be significant with a larger group, the results show that the facilitation effect was larger in the young in this paradigm in contrast to the larger facilitation effect seen in the elderly in the previously published results. Our results are also consistent with the notion that elders have increased variability which can be seen by the larger range of RTs in the quantile plot of Figure 1 [e.g. the RTs are very similar across age (<25 ms difference) at the lower quantiles but the difference is larger at the larger quantiles (90-100 ms at 0.95 quantile)].

The multisensory enhancement reported for area STG in the young is consistent with previous results from a number of investigators who also found enhancement in the auditory association area [3,7]. The results in the elderly are consistent with a study comparing normal elderly with hearing impaired elderly. Musacchia et al. [14] found that $A+V > AV$ in a waveform comparison in the adults with normal hearing (displaying a sub-additive effect). These results, combined with previous results reported in the young, provide additional evidence that a transition from super-additive to sub-additive multisensory responses occurs across the life span in some experimental conditions. Understanding how changes in multisensory processing interacts with known changes in sensorimotor processing, which likely contributes to a main effect of longer RTs in the elderly [27], is important for fully understanding how the elderly brain compensates for sensory amplitude and latency changes across the lifespan.

Conclusion

The results of this study suggest that the STG area in the elderly responds differently to multisensory integration compared to young adults, consistent with decreased facilitation in the behavioral responses in the elderly. The comparison between multisensory responses and unisensory responses allows us to factor out peripheral sensorimotor changes as an explanation of the changes identified in area STG and suggest that the cortical response to AV integration changes with age. As an extension to the current work, it would be interesting to employ a paradigm similar to that performed by Diederich and Laurienti where the elderly are expected to perform better in the multisensory integration RTs than the young to determine if the STG amplitude differences reversed in the case where the elderly benefit from multisensory integration relative to the young. Differences between the current results and previous psychophysical results suggest that parametric examinations of multisensory integration across the lifespan would provide insight into how the aging brain adjusts to both peripheral and central slowing across the lifespan. Future studies also need to focus on how the full multisensory cortical network corresponds with behavioral results.

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Figure 1.

Cumulative distribution functions for the AV reaction times and the RACE model predicted RTs (AVpred) for the young (Y - solid and dotted lines) and elderly (E - circles and boxes), respectively. The significant facilitation is denoted by the grayed in area between the AV Y and AVpred Y lines. There were no quantiles at which the elderly showed significantly greater facilitation than the race model.

Figure 2.

The averaged timecourses from area STG obtained after performing multi-dipole modeling. The timecourses across participants within age category and condition were averaged together. Elderly – blue line, young – red line.

Table 1

a. RTs Young versus Elderly			
	A	V*	AV**
<i>Young (N = 8)</i>	499	442	421
<i>Elderly (N = 8)</i>	534	493	478

b. Percent Correct Young vs. Elderly			
	A	V	AV
<i>Young (N = 8)</i>	89	95	93
<i>Elderly (N = 8)</i>	80	95	95

significantly different than A condition

*
p < 0.03

**
p < 0.003