

The effects of aging on the brain activation pattern during a speech perception task: an fMRI study

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Abstract In the present study, brain activation associated with speech perception processing was examined across four groups of adult participants with age ranges between 20 and 65 years, using functional MRI (fMRI). Cognitive performance demonstrates that performance accuracy declines with age. fMRI results reveal that all four groups of participants activated the same brain areas. The same brain activation pattern was found in all activated areas (except for the right superior temporal gyrus and right middle temporal gyrus); brain activity was increased from group 1 (20–29 years) to group 2 (30–39 years). However, it decreased in group 3 (40–49 years) with further decreases in group 4 participants (50–65 years). Result also reveals that three brain areas (superior temporal gyrus, Heschl's gyrus and cerebellum) showed changes in brain laterality in the older participants, akin to a shift from left-lateralized to right-lateralized activity. The onset of this change was different across brain areas. Based on these findings we suggest that, whereas all four groups of participants used the same areas in processing, the engagement

and recruitment of those areas differ with age as the brain grows older. Findings are discussed in the context of corroborating evidence of neural changes with age.

Keywords fMRI · Speech perception processing · Neural deterioration · Brain laterality

Introduction

Before the era of functional imaging, behavioral methods and interpretive logic of clinical neuropsychology guided brain-based theories of cognitive aging. This approach assumes that minimal age differences in behavioral performance infer minimal alterations in underlying cognitive mechanisms. However, in the era of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), the underlying neural mechanisms in the form of neural activity patterns can be measured during cognitive processing. Therefore, researchers such as Grady et al. [1] and Reuter-Lorenz and Cappell [2] discovered that it is incomplete or even erroneous to assume that cognitive aging is a process of progressive mental loss which is linear throughout the life. Furthermore, previous research suggests that some aspects of age-related cognitive decline begin in healthy, educated adults when they are in their 20s and 30s [3]. Although the behavioral performance is comparable between the young and older participants, there are changes in all brain levels, from molecules to morphology. Therefore, it is important to get a clearer and more complete understanding of the neural changes associated with the processes of normal aging. The present study examined the neural underpinnings of cognitive aging by comparing the cortical neurophysiological characteristics of speech perception (SP) processing in four

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groups of participants ranging in age between 20 and 65 years. Some background is first presented.

The effects of aging on verbal SP processing have been studied using a variety of functional imaging modalities including electroencephalography (EEG), fMRI, and magnetoencephalography (MEG) [4]. One fMRI study demonstrated reduced activation in Perisylvian regions in older participants during speech perception tasks [5]. This neural change was suggested to be associated with speech processing which may result in decreased task efficiency or the recruitment of alternative networks to support speech function [6, 7]. Furthermore, Wlotko et al. [7] reported that activity of the bilateral superior temporal gyrus (STG) including Brodmann's area (BA) 22 declines in older participants during the processing of a speech perception task; moreover, activity in the left hemisphere decreased more than in the right hemisphere. Therefore, it appears that the right hemisphere was activated more than the left hemisphere in the older participants on the same task. This situation can also be explained in terms of the right hemi-aging hypothesis according to which age-related cognitive declines affect functions attributed to the right hemisphere to a greater degree than those associated with the left hemisphere [8]. Evidence has led to the further suggestion that the decrease of left-hemisphere involvement in the older brain (as compared to the right hemisphere which shows higher activity) during verbal speech processing tasks is due to deterioration of the neural networks involved in speech processing [9]. This may be an attempt to compensate and recruit additional networks or the result of specific areas which are no longer easily accessed. The ability to augment processing in these specialized (left lateralized) regions by recruiting the homologous areas of the contralateral regions might be in response to neural decline or insult. Furthermore, the phenomenon of contralateral recruitment of the brain areas in response to brain injury has been documented in both acute and progressive neurodegenerative disorders [10, 11]. In contrast, such contralateral recruitment is not consistent with the Gillard et al. [12, 13] studies which did not find an association between increasing age and recruitment of the contralateral areas.

As mentioned above, aging is associated with cortical and subcortical neural changes. Such changes could affect the neurophysiological and behavioral measures of speech perception processing. Furthermore, age-related reductions in speech processing have been reported across a wide variety of tasks including those that require speeded decisions, category judgments, and stem completions [7]. Although general reading ability and knowledge are well preserved into old age, the speed and efficiency with which speech processing judgments are made appear to peak in young adulthood and then decline thereafter [7].

The focus of this paper is on the effects of age on speech perception with the specific aim to examine and compare speech perception processing across four groups of healthy right-handed participants of different ages. If task demands are more difficult to meet in older age due to changes in neural processing, we would expect to see changes in brain recruitment (brain activation or brain dominance laterality) in the older groups. In contrast, if speech stimuli processing does not tax older people any more than younger, we might expect to see all groups of participants activating the same brain areas with comparable activation intensity (number of activated voxels and t value).

Materials and methods

Participants

Fifty-four Malay male right-handed [14] adult participants, ranging in age from 20 to 65 and divided into four age groups (see Table 1) participated in this study. The average scores of the Edinburgh Inventory for each group are shown in Table 1 and statistical analysis (ANOVA) revealed no significant differences on average score across the four age groups. Participants had normal hearing and were free of tinnitus and neurological disease. The older adults (age 50 and above) were also given the mini mental status examination (MMSE) [15], with all of them scoring in the normal range between 28 and 30. After full explanation of the nature and risks of the study, written informed consent was obtained from all participants in accordance with the protocol approved by the Institutional Ethics Committee (IEC) of the Universiti Kebangsaan Malaysia. (Reference no: UKM 1.5.3.5/244/NN-075-2009).

Audiometry

Prior to the fMRI scan, a standard questionnaire and online audiometric measures were obtained from all participants (Rochester Hearing and Speech Center and (<http://myhearingtest.net/>)). Participants had hearing thresholds in a normal limit in the frequency range relevant for speech stimuli [16]: (250, 500, 1,000, 2,000, 3,000, 4,000 and 8,000 Hz).

Data acquisition

This study was conducted in the Department of Radiology, UKM Medical Centre, using a 1.5-T magnetic resonance imaging (MRI) system (Siemens Magnetom Avanto) equipped with functional imaging options and echo planar imaging capabilities. A radiofrequency (RF) head coil was used for signal transmission and reception. Prior to the functional imaging scans, structural T1-weighted images

Table 1 Demographic and performance data obtained from 54 participants

Age groups	Group 1 20–29	Group 2 30–39	Group 3 40–49	Group 4 50–65
<i>N</i>	15	15	10	14
Age (range)	23–29	30–37	41–47	50–65
Age (mean \pm SD)	27 \pm 2.18	33 \pm 2.18	45 \pm 2.28	59 \pm 2.65
Years of education (mean \pm SD)	14.80 \pm 0.79	15.40 \pm 1.50	13.90 \pm 3.16	13.00 \pm 2.46
SP, performance accuracy (mean \pm SD)	15.49 \pm 2.28	16.71 \pm 2.26	13.34 \pm 4.50	13.52 \pm 3.57
Average score of Edinburgh Inventory (mean \pm SD)	73 \pm 8.70	83 \pm 3.60	79 \pm 1.20	81 \pm 5.90

SP speech stimuli task

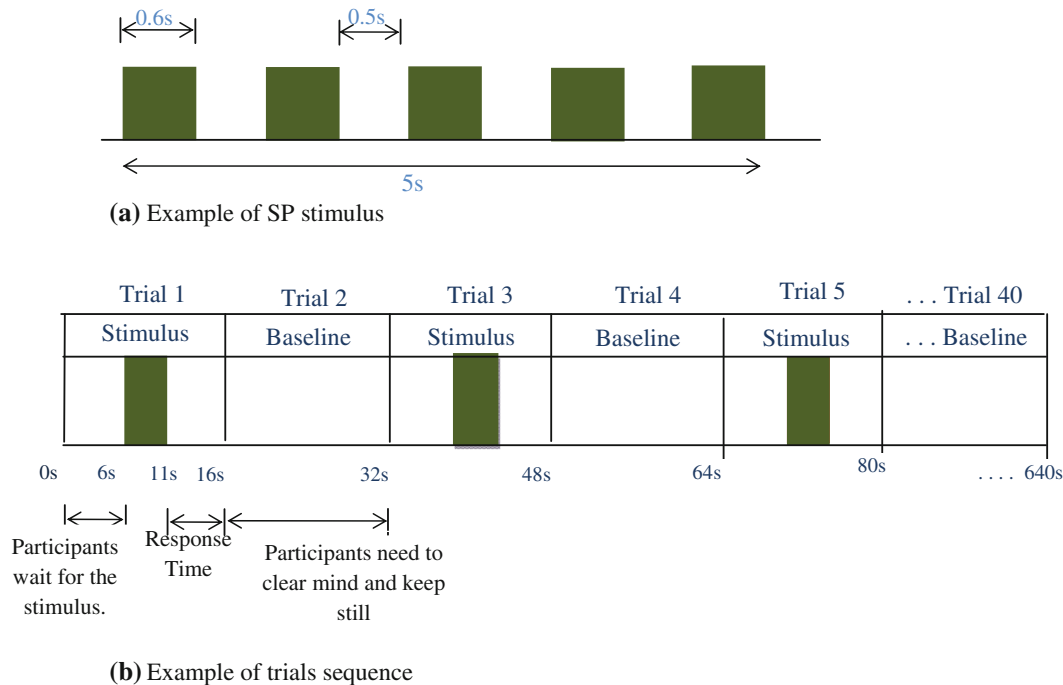


Fig. 1 **a** Illustration of stimulus train consisting of a sequence of five unrelated familiar words (verbs and nouns were randomly selected) to produce the speech stimuli. **b** The sequence of the conditions was fixed as follows: speech stimuli; baseline; speech stimuli; baseline.

During the stimulus trials, stimuli were presented at the 6th second, and lasted approximately 5 s, and participants were given 5 s to repeat forward all the five words presented. Total duration of each trial is 16 s

were acquired using multi-planar reconstruction (MPR) spin-echo pulse sequence with the following parameters: TR = 1,240 ms, FOV = 250 mm \times 250 mm, flip angle = 90°, matrix size = 128 \times 128 and slice thickness = 1 mm. Functional images were then acquired using a gradient echo–echo planar imaging (GRE-EPI) pulse sequence. Each whole-brain acquisition consisted of 21 axial slices covering all brain regions including the cerebellum. The following parameters were used for the functional scans: repetition time (TR) = 2,000 ms, echo time (TE) = 50 ms, field of view (FOV) = 192 \times 192 mm, flip angle (α) = 90°, matrix size = 128 \times 128 and slice thickness = 5 mm with 1.25 mm gap. A sparse temporal sampling was used to avoid the interference of scanner sound onto the stimulus [17].

Task materials

The speech stimuli consisted of a series of natural speech words produced by a Malay male adult and were digitally recorded (Sony Digital Voice Editor), stored and edited using Adobe Audition 2.0 software. An intensity level of 55 dB SPL was used for stimulus presentation.

Experimental design

A total of 30 (2-syllable and 3-syllable) unrelated familiar Malay words (verb and nouns) were randomized to produce each 20-trial set of speech stimuli. Figure 1a shows an example of the speech trial which consists of five consecutive 0.6 s duration stimuli separated by 0.5 s of silence,

making up a total stimulus time of 5 s per stimulus train. During a trial, the stimuli were presented at the 6th second and lasted approximately 5 s, as in Fig. 1b. During the speech task, participants were given 5 s to repeat forward all the five words presented. Figure 1b shows examples of trial sequences. There were 40 trials in total, each lasting 16 s duration, making up 20 speech trials (stimulus) and 20 trials with no stimulus (baseline).

Before a participant entered the MRI scanner, instructions about the task were explained in detail and it was emphasized that participants were to focus with an otherwise clear mind throughout the procedure and to keep still. During scanning, participants lay comfortably in a supine position in the MRI scanner. An adjusted head holder restricted head movement. Auditory stimuli were presented through earphones.

Each individual participant's scores were recorded manually by an experimenter in the console room (i.e., number of correct forward repetition trials).

Data analysis

Each participant's cognitive performance was scored as the mean of the series of words correctly repeated. Repeated measure analyses of variance (ANOVAs) (SPSS 20.0 statistical software package) were then conducted on all participants' data using age group as a between-subjects factor, to evaluate age-related differences on performance accuracy. The data were further analyzed using post hoc Tukey tests to evaluate which groups show age-related differences. Linear regression was used to evaluate the performance accuracy versus age across four groups of participants. All the statistical analyses were corrected for multiple comparisons using Bonferroni ($p < 0.01$).

For fMRI data processing, our sparse-imaging data were analyzed using MATLAB 7.4—R2008a (Mathworks Inc., MA, USA) and Statistical Parametric Mapping (SPM8) (Functional Imaging Laboratory, Wellcome Department of Imaging Neuroscience, Institute of Neurology, University College of London, UK; <http://www.fil.ion.ucl.ac.uk/spm>). The first two images of every EPI-recording session were discarded to account for the approach to steady state of the MR signal. Prior to image analysis, each participant's raw data were motion corrected and normalized [18–20]. The amount of absolute motion did not exceed 2 mm for any participant. Three participants' data were discarded from data analysis due to excessive motion. Data were further analyzed using a 12-parameter non-linear normalization into the MNI-reference state as implemented in SPM8, with smoothing (FWHM = 6 mm). The fMRI data were analyzed according to the general linear model as implemented in SPM8. With regard to the different conditions, two regressors were included in the design: speech (SP) and baseline (Q). The regressors were convolved using the

hemodynamic response function as provided in SPM8. Statistical analysis was performed using a mixed effects model; fixed effects analysis (FFX) was used for single participant analysis and random effects analysis (RFX) for group analysis. For group analysis, contrast images were computed for each participant, and then one-sample *t* tests were performed. For FFX analysis, statistical significance was set at $p < 0.05$, emerging from whole-brain analyses. For RFX analysis, statistical significance was set at $p < 0.05$ cluster level [21]. Finally, the region of interest (ROI) approach was used, focusing on the cortical brain region with a minimum cluster size of 15 voxels and $p < 0.05$ at cluster size defined using automatic anatomic templates derived from the toolbox WFU pickatlas [22]. The rationale of using the cut-off with minimum 15 voxels and $p < 0.05$ at cluster level is to discard the unwanted voxels. This is due to too many activation areas activated with a voxel cluster size below 15.

The laterality index (LI) was calculated using the formula $LI = (V_L - V_R)/(V_L + V_R)$, in which V_L is the number of the activated voxels in the left hemisphere and V_R is the number of activated voxels in the right hemisphere. The LI ranges from -1 to 1 from which the values between -1 and 0 indicate right-hemisphere dominance and from >0 to 1 indicate left-hemisphere dominance [23].

Results

Behavioral data

Behavioral data (performance accuracy) collected during the fMRI sequences for the speech perception (SP) task for the four groups of participants are presented in Table 1. The data show a significant main effect of age group on behavioral scores $F_{(3,50)} = 10.41$, $p = 0.001$. Statistical analysis using Tukey comparisons further revealed differences between group 1 and group 3 ($p = 0.006$), group 1 and group 4 ($p = 0.003$) and group 2 and group 3 ($p = 0.004$), where group 1 refers to the youngest group and group 4 to the oldest as shown in Table 1. However, the comparisons between group 1 and group 2 and group 3 and group 4 did not reach significance. A further analysis using linear regression was conducted to evaluate the age-related effects on behavioral scores, revealing a significant effect ($R^2 = 0.561$, $F_{(1,52)} = 23.82$, $p = 0.001$). Hence, the present results clearly demonstrate decreases in performance accuracy with increasing age for the SP task.

Activated brain areas across age

Results of the present study reveal that all four groups of participants recruited the same brain areas including the

Table 2 Anatomical area, brain hemisphere, *t* value, laterality index (LI) value, coordinates of maximum intensity (*x*, *y*, *z*), and number of activated voxels are obtained from group analysis (*p* < 0.05 at cluster level); across four group of participants during speech stimuli task (SP)

Anatomical area	Hemisphere	20–29			30–39			40–49			50–65						
		<i>t</i> value	Coordinate (<i>x</i> , <i>y</i> , <i>z</i> mm)	NOV	LI	<i>t</i> value	Coordinate (<i>x</i> , <i>y</i> , <i>z</i> mm)	NOV	LI	<i>t</i> value	Coordinate (<i>x</i> , <i>y</i> , <i>z</i> mm)	NOV	LI				
STG	L	6.61	-60, -12, 12	276	0.26	13.13	-56, -6, 0	1,504	0.11	12.72	-58, -20, 2	571	0.14	6.04	-58, -32, 10	253	-0.35
	R	7.23	46, -24, -4	160	12.45	64, -10, 6	1,192	14.30	14.30	54, -16, -8	430	8.11	8.11	64, -18, 0	535		
MTG	L	5.59	-54, -28, 4	122	0.65	9.90	-62, -14, 0	298	0.85	8.49	-58, -20, 0	145	0.14	5.91	-58, -32, 8	106	1.00
	R	4.92	-48, -22, 8	25	6.15	69, -20, -4	23	11.42	11.42	52, -16, -10	108	-	-	-	-	-	-
PCG	L	5.09	-50, -4, 46	106	0.64	8.71	-54, -6, 34	737	0.30	8.79	-42, 2, 38	203	0.15	7.83	-42, -8, 44	105	0.34
	R	4.64	50, -8, 36	23	9.24	50, -4, 40	393	6.66	6.66	46, 0, 34	148	5.68	5.68	44, -6, 42	51		
Cerebellum	L	5.34	-4, -74, 24	42	0.09	8.18	-24, -62, 28	469	-0.15	10.23	-40, -68, 28	51	-0.35	-	-	-	-1.00
	R	6.40	26, -64, 30	35	9.69	34, -60, -30	646	8.86	8.86	36, -58, -32	108	4.59	4.59	38, -78, 24	19		
Post-CG	L	7.67	-62, -10, 14	300	0.34	9.56	-56, -6, 16	530	0.40	8.19	-58, -2, 20	66	-0.05	6.96	-44, -10, 40	99	1.00
	R	5.25	56, 10, 22	145	8.19	56, -4, 30	227	6.31	6.31	56, -2, 22	73	-	-	-	-	-	
Heschl gyrus	L	5.58	-32, -30, 10	37	1.00	6.08	-36, -30, 14	185	0.19	6.55	-48, -16, 6	42	0.61	4.61	-42, -26, 10	11	-0.47
	R	-	-	-	6.92	40, -20, 6	124	5.57	5.57	60, -4, 6	10	6.69	6.69	64, -4, 6	31		

For the LI value, the positive value indicates left lateralization and negative value indicates right lateralization of brain asymmetry

-, not significant

L left, R right, NOV number of activated voxels, LI laterality index value, STG superior temporal gyrus, MTG middle temporal gyrus, PCG precentral gyrus, IFG inferior frontal gyrus, MFG middle frontal gyrus, IPL inferior parietal lobes, SPL superior parietal lobes, Post-CG postcentral gyrus, HG Heschl gyrus

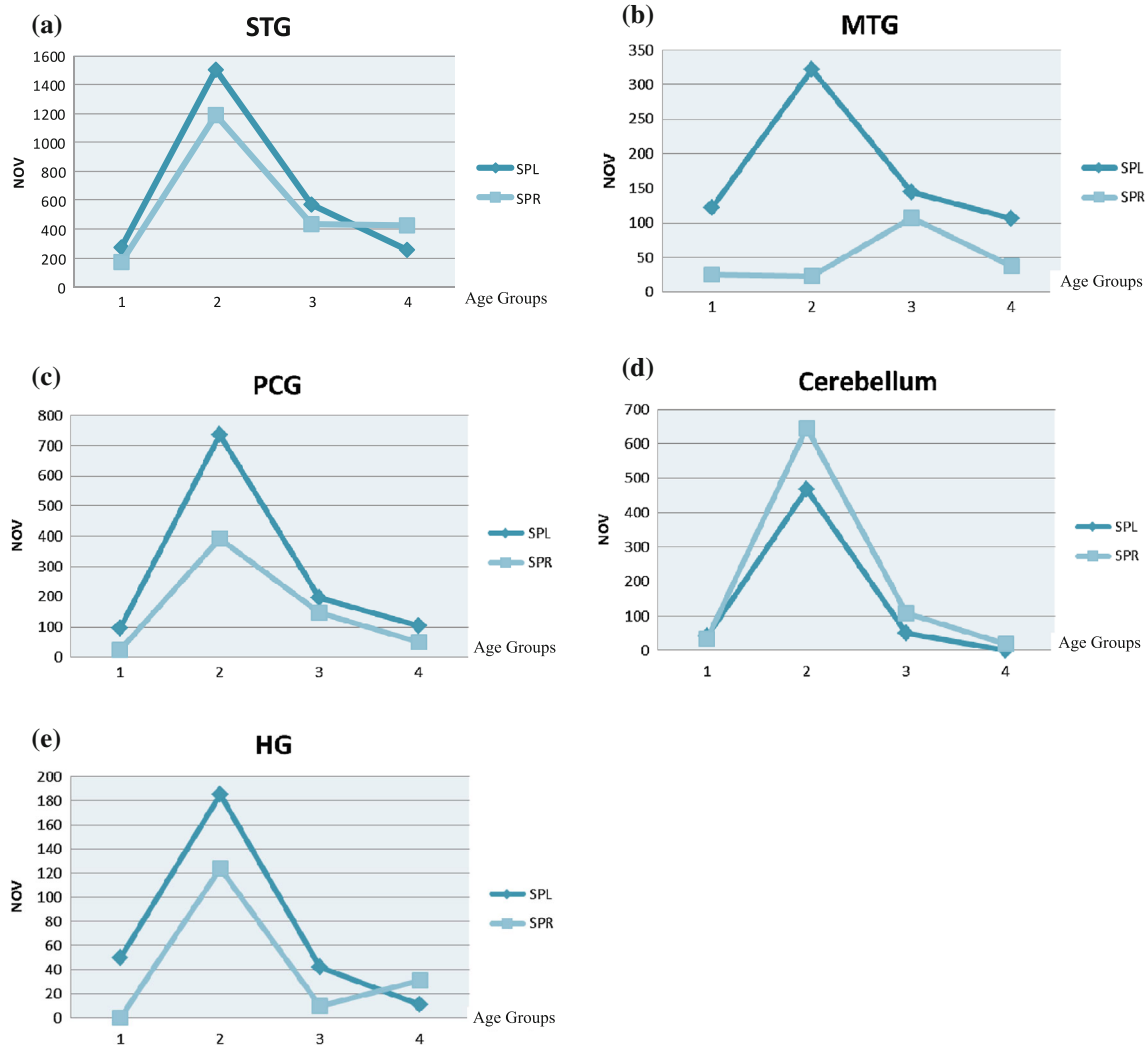


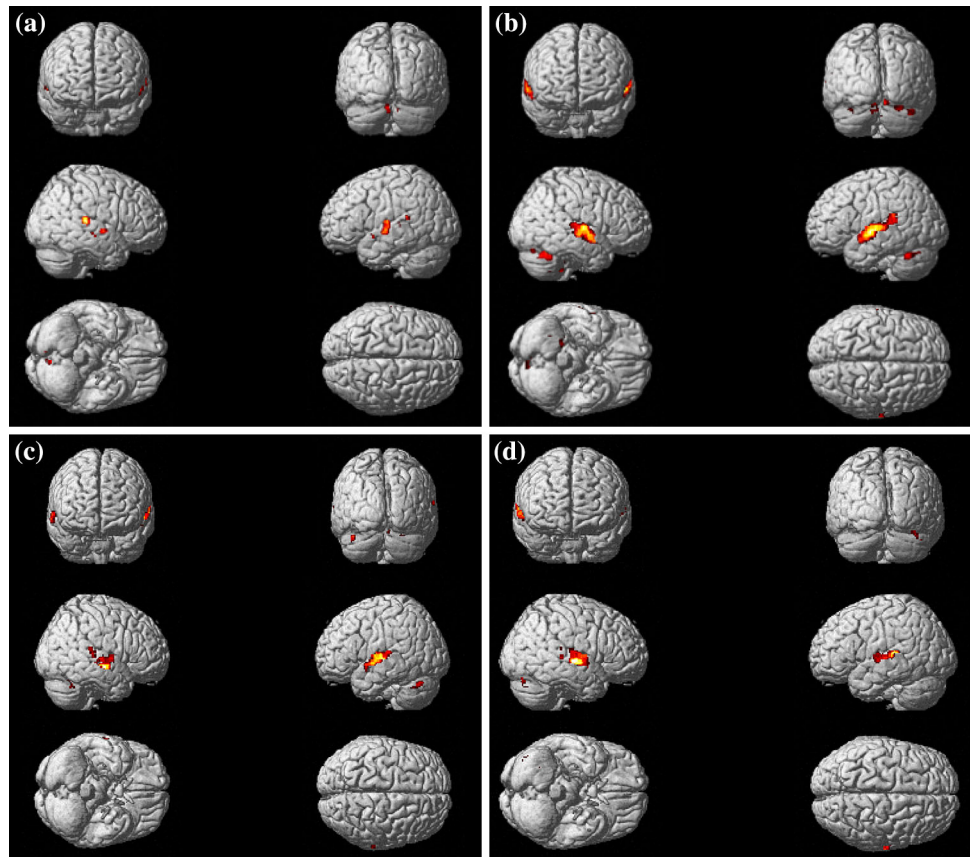
Fig. 2 Plot shows brain activation pattern of five brain regions during SP task on four groups of participants: **a** STG, **b** MTG, **c** PCG, **d** cerebellum and **e** HG

bilateral superior temporal gyrus (STG), middle temporal gyrus (MTG), precentral gyrus (PCG), postcentral gyrus (post-CG), cerebellum and Heschl's gyrus (HG) during the speech perception (SP) task. Age-related differences were primarily observed in three areas including the right MTG, right post-CG and left cerebellum, all of which were not activated to a statistically significant level in group 4 participants (the oldest group) as tabulated in Table 2. The brain activation pattern of all activated areas (except in right STG and right MTG) across the four age groups demonstrated the same pattern of brain activity. Specifically, the number of activated voxels (NOV) increased from group 1 (20–29 years) to group 2 (30–39 years), and this NOV is at peak in group 2 participants. However, the NOV then decreased in group 3 (40–49 years) and further decreased in group 4 participants (50–65 years); the pattern of NOV across the four age groups is plotted in Fig. 2c–e.

For the right STG, an increase in NOV was found between group 1 and group 2, with a decrease in group 3 but again an increase in group 4 participants (as plotted in the Fig. 2a). Finally, for the right MTG, results demonstrate an increase of NOV across age groups, but the activation was not significant in group 4, as shown in the Table 2 and plotted in Fig. 2b. The NOV, *t* value and laterality index (LI) value of each brain region for each age group are tabulated in Table 2.

Results on the L1 calculation reveal strong associations between aging and decreased left-lateralized activity of brain areas in STG, cerebellum and HG (as in Table 2; Fig. 3). These areas appear to shift to being more right lateralized in the older groups of participants. However, the onset of changes from left lateralized to right lateralized varies from one area to another. Results also reveal that both hemispheres contributed to these lateralized changes, i.e.,

Fig. 3 Activation maps showing the averaged activated volume of BOLD signal of STG, HG and cerebellum across the four groups of participants: **a** 20- to 29-year olds, **b** 30- to 39-year olds, **c** 40- to 49-year olds and **d** 50- to 65-year olds (note: left side of the brain is on the *left*: neurological conventions)



brain activity was not decreased equally in both hemispheres but rather, it decreased more in the left hemisphere.

Discussion

The present study demonstrates age-related brain changes during normal aging using a speech perception (SP) task. These changes are in the form of increased and decreased brain activity and shift in brain lateralization with age in four non-overlapping age groups of healthy right-handed participants; group 1 (20–29 years), group 2 (30–39 years), group 3 (40–49 years) and group 4 (50–65 years). The brain areas implicated in the lateralization shift are the STG, cerebellum and HG, all of which appear to shift in lateralization from left to right with age in the older groups. Other activated areas such as the MTG, PCG and post-CG remain left lateralized across the four age groups.

Activated areas across the four age groups

The SP processing appears to activate a brain network which includes the STG, MTG, HG, PCG, cerebellum and Post-CG in all four groups of participants. Results showing bilateral activation of the STG, including the primary

auditory cortex, are consistent with other studies using auditory speech stimuli [24, 25, 26, 27, 28]. The present results also show strong activation in the MTG bilaterally. MTG has been consistently associated with phonological processing [29, 30, 31, 9]. In addition to the auditory speech areas, results also reveal activation of the cerebellum (bilaterally). The cerebellum is suggested to be linked to cognitive processing involved in phonological processes [32, 33, 34]. Significant activation of the cerebellum is also consistent with other studies that have found activation of bilateral cerebellum in reading and language tasks [33, 35]. The PCG and Post-CG were also activated during the SP task. The activation of these areas was expected, as participants were asked to repeat forward all the five words presented. Furthermore, SP processing used in the present study also involves memory mechanisms, in which participants need to remember the words presented to repeat them back. Both areas bilateral PCG and Post-CG are important for rehearsal of verbal information during memory processes [36, 37]. Although the same neural areas were activated during the task in all four groups of participants, the present results demonstrate differences in NOV, *t* value and LI values. These results strongly suggest that older participants engage and recruit brain areas differently than younger participants to accomplish the same task.

The present study using SP task found that brain activity was increased from group 1 to group 2 participants in all activated areas bilaterally. The increases of brain activity in these two groups (group 1 to group 2) are proposed to reflect possible compensatory processes associated with normal aging. The idea that such compensatory processes are involved is further supported by the behavioral performance. Specifically, behavioral performance demonstrates no significance difference in performance accuracy between group 1 and group 2, however, brain activity demonstrated differences between the two groups. As people age, it is known that changes take place, including atrophy in gray and white matter, synaptic degeneration, and neurochemical alterations [5, 38]. Such changes might result in increased processing demands during the task. Therefore, the brain recruits more resources (e.g., activated regions) to accomplish the same task.

However, results demonstrate that brain activity began to decrease in group 3, and further decreased in group 4 participants. The same brain activation pattern can be seen in all activated areas except the right STG and right MTG. Right STG showed increased brain activity in group 4 participants and the right MTG showed increased brain activity across the age groups. These patterns of brain activation in group 3 and group 4 participants (except for right STG and right MTG) might be related to neural changes in the form of structural or volumetric effects with age [39]. Furthermore, based on the long-standing model of neurocognitive aging on the lesioned brain, performance deficits might have arisen from diminished contributions of specialized brain regions in older participants, given the possibility of atrophy and a reduced ability to engage the relevant neural circuitry; this would result in less brain activation in older participants as compared to the younger participants in performance of the same task [40]. The present results on brain activity are further supported by the decrease in behavioral performance accuracy with age, providing strong support for the notion that the brain undergoes a series of changes during aging [5, 41]. Our results also suggest that changes occurring in the younger ages (i.e., those differentiating groups 1 and 2) reflect different processes than those occurring in the older groups (i.e., differentiating groups 3 and 4 from the younger participants). Peaks in processes of reorganization might occur earlier in life, and those might be followed by declines related to aging.

Examination of the brain asymmetry (LI calculation) indices per region showed key regions in the brain had left-lateralized activity in all four groups of participants, with the exception of the STG, cerebellum and HG in older groups of participants (which were right lateralized). Findings of left-lateralized activity during speech perception processing are in agreement with previous research [42, 27, 43] indicating

that brain regions critical for language perception, comprehension, production and processing are typically located in the left hemisphere for the right-handed participants.

Age-related brain activation in the present study identified three areas (STG, cerebellum and HG) revealing changes from left-lateralized to more right-lateralized activity in the aging brain. The present results demonstrate a similar pattern of neural response across the four age groups in STG and HG. However, while age groups 1, 2, and 3 showed predominantly left-lateralized activity, this pattern of neural response changed in group 4 (the oldest group) to being more right lateralized. In the cerebellum, the lateralization changes occurred earlier in age, with an observed change began already in group 2. According to the present results, we propose that the approximate age of onset of lateralization changes depends on the sensitivity of the particular area to a given task. It is possible that some form of neural decline which occurs during aging is responsible for the apparent shift in lateralization in the older adults. Indeed, the cognitive data also reveal decreasing performance accuracy with increasing age (which will be discussed in more detail below).

It is known that with aging, there is also evidence of synaptic degeneration and neurochemical alteration [44–45]. In addition, there is a slowing of processing time which might affect component operations involved in the SP task [46–48]. It is, therefore, possible that the shifts in laterality are part of a reorganization of brain processes associated with alternate patterns of brain recruitment which capitalize on interhemispheric communication and function. Decreases in left-lateralized activity during the SP task in older participants might, therefore, reflect an age-related difficulty in recruiting specialized neural mechanisms, and/or may be associated with a reduced computational capacity for speech processing (or memory associated with such processing) in older adults [49–51]. All of these factors might contribute to an increased processing demand in older adults as compared to younger adults on the same task. The shift in recruitment to right-hemisphere processes might, therefore, allow for information to be spread across a larger processing space; moreover, cooperation between hemispheres not only allows subcomponents of a task to be handled by different processors (hemispheres), but might even allow for some parallel processing [52]. In contrast, when a task is simple enough to be handled by a single hemisphere, cross-hemispheric processing might not be efficient or necessary.

Conclusions

The present study examined age-related effects on a task involving speech stimuli and memory processing of speech

in groups of adults separated into four non-overlapping age groups. All four groups of participants activated the same brain regions, which suggests that while participants employ the same brain areas, the engagement and recruitment of areas changes with increasing age. All activated areas (except the right STG and right MTG) show the same pattern of brain activity; they peaked in group 2 participants, and then decreased in group 3, with further decrease in group 4 participants. Three brain regions (STG, cerebellum and HG) demonstrated changes in brain laterality in which a predominantly left-lateralized pattern (normally in right-handed participants) of activity shifted to a more right-lateralized pattern with increasing age. Other activated brain areas (PCG, Post-CG and MTG) remained left lateralized across the age groups. Cognitive performance demonstrated that older participants performed less accurately than younger participants. In our view, the present findings reveal evidence of reorganizing processes of brain function across the age groups.

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Conflict of interest The author certify that there is no actual or potential conflict of interest in relation to this article.

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