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Age-related effects on the neural processing of semantic complexity in a continuous narrative: Modulation by gestures already present in young to middle-aged adults

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ABSTRACT

The processing of semantically complex speech is a demanding task which can be facilitated by speech-associated arm and hand gestures. However, the role of age concerning the perception of semantic complexity and the influence of gestures in this context remains unclear. The goal of this study was to investigate if age-related differences are already present in early adulthood during the processing of semantic complexity and gestures. To this end, we analyzed fMRI images of a sample of 38 young and middle-aged participants (age-range: 19–55). They had the task to listen and to watch a narrative. The narrative contained segments varying in the degree of semantic complexity, and they were spontaneously accompanied by gestures. The semantic complexity of the story was measured by the idea density. Consistent with previous findings in young adults, we observed increased activation for passages with lower compared to higher complexity in bilateral temporal areas and the precuneus. BOLD signal in the left frontal and left parietal regions correlated during the perception of complex passages with increasing age. This correlation was reduced for passages presented with gestures. Median-split based post-hoc comparisons confirmed that group differences between younger (19–23 years) and older adults within the early adult lifespan (24–55 years) were significantly reduced in passages with gestures. Our results suggest that older adults within early adulthood adapt to the requirements of highly complex passages activating additional regions when no gesture information is available. Gestures might play a facilitative role with increasing age, especially when speech is complex.

1. Introduction

1.1. The aging brain and communication

Age impacts the efficiency of communication even in the absence of disease. For example, language production is one domain influenced negatively by age. Evidence suggests impairments in word production, as well as reduction of syntactic and semantic complexity during sentence production (Burke et al., 1991; Feyereisen, 1997; Heine et al., 1999; Kemper and Sumner, 2001). Whereas most of these functions decline in old age (>60 years), some functions requiring, for example, verbal working memory start to decline already very early in young or middle-aged population (Park et al., 2002). In contrast, language perception and comprehension is a fundamental ability that seems to remain relatively intact despite increasing age (Thornton and Light, 2006; Burke and Shafto, 2008; Tyler et al., 2010). Behavioral studies about the influence of age on semantic processing reported very subtle age-related effects (Mayr and Kliegl, 2000), probably because the conceptual representations of words remain well preserved (Burke and Shafto, 2008). Besides, there is evidence that vocabulary and general knowledge even improve during advancing adulthood and may thus support the processing of language (Kemper and Sumner, 2001).

Nevertheless, brain-weight loss, white matter disruption, reduced grey matter density and reduced network connectivity are some of the structural effects of aging (Sowell et al., 2003; Raz et al., 2004, 2005; Sullivan and Pfefferbaum, 2006; Gunning-Dixon et al., 2009). These

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changes affect a range of functions such as working memory, inhibitory functions, long term memory among others. For example, the changes in speed processing and in working and long-term memory start from the 20s, and the decline in the following years is continuous (Park et al., 2002; McNab et al., 2015).

The main goal of our study was to analyze if age-related differences are already present in early adult lifespan within a group of young to middle-aged participants regarding the processing of semantic complexity given the continuous cognitive decline. Besides, it was investigated if the presentation of gesture information would facilitate the processing of semantic complexity, thus reducing the age-related differences.

1.2. Compensatory mechanisms

Considering the evidence about the continuous cognitive decline, the question that arises is how the brain manages to process language and achieve cognitive demanding functions despite these changes. The brain remains adaptive across the adult lifespan, reflected by compensatory strategic mechanisms that stabilize performance. Several compensatory mechanisms have been proposed in the literature.

One of the major compensatory mechanisms is the bilateral recruitment of the human brain. Bilateral activation in older adults, in comparisons to unilateral responses by younger adults, have been reported in several PET and MRI studies (Cabeza et al., 1997; Reuter-Lorenz et al., 2000; Morcom et al., 2003). Besides, the additional recruitment of prefrontal regions has also been proposed as a compensatory mechanism supporting several cognitive processes (Grady et al., 1994; Davis et al., 2008). The reason why the frontal regions are recruited as a compensatory mechanism remains unclear considering that this region is subject to pronounced decline during aging (Raz et al., 1997; Fera et al., 2005; Geerligs et al., 2015). Some authors accentuated the versatile and general characteristics of this region and its favorable connectivity with other regions. These properties might enable the support of cognitive demanding tasks (for review see Park and Reuter-Lorenz, 2009; Shafto and Tyler, 2014).

Other studies described parietal regions activation as a compensatory mechanism in older adults. For example, Fera et al. (2005) investigated age differences in probabilistic category learning and observed increased activation in parietal regions in older adults. Besides, internal connectivity loss within the frontoparietal network and reduced grey matter in parietal regions seem to be caused by aging (Good et al., 2001; Resnick et al., 2003; Geerligs et al., 2015). Thus, the strategies could reflect the development of new pathways in order to accomplish demanding tasks and the increase of connectivity between networks given the reduction of internal network connectivity (Geerligs et al., 2015). For example, the default mode network (Raichle et al., 2001) (DMN, hereafter), which has been associated with the processing of low complexity segments of a narrative (Cuevas et al., 2019), is a network strongly affected by age (Mevel et al., 2013; Geerligs et al., 2015). Andrews-Hanna et al. (2007) reported anterior-posterior disruption within the DMN by increasing age, even in the absence of disease. Grady et al. (2006) described less suppression of DMN during a cognitive demanding task in older adults.

Thus, compensatory mechanisms have been reported by aging studies concerning the production and the processing of language (Wingfield and Grossman, 2006). However, a study investigating the effects of age during the perception of a narrative varying in terms of complexity would complement the research and provide useful information about the situations such mechanisms are evoked.

1.3. Measuring linguistic complexity changes

Changes in linguistic complexity due to increasing age have been investigated using diverse complexity metrics (Cheung and Kemper, 1992). One of them, the idea density (ID, hereafter), measures how many propositions are expressed by written or spoken language in relation to the number of words required to express them. Thus, ID as an index of communication efficiency (Chand et al., 2012b) has been used in several longitudinal studies analyzing aging, cognitive decline and, mental disorders (Snowdon et al., 1996; Kemper et al., 2001; Riley et al., 2005; Engelman et al., 2010; Roark et al., 2011; Spencer et al., 2012, 2014; Bryant et al., 2013; Moe et al., 2016). High ID scores are seen as an indicator of cognitive reserves (Engelman et al., 2010), and people with high ID scores in early life are less likely to develop Alzheimer disease in later life (Snowdon et al., 1996).

In contrast to production, the perception of semantic complexity measured by the ID has not been investigated intensively yet. To our knowledge, the only study analyzing the neural correlates of the perception of ID comes from our group (Cuevas et al., 2019). The study revealed complexity dependent attenuation of DMN and a pronounced supporting effect of gestures when cognitive demands are high. The production of ID within older populations has been approached by several studies (Snowdon et al., 1996; Kemper et al., 2001; Engelman et al., 2010; Spencer et al., 2012, 2014), and a negative relation between the production of ID and age can be assumed. Therefore, a study measuring the age effects on the perception of ID could contribute to the understanding of the aging brain. Despite the extensive interests in age-related effects on language, the research topic has been approached through very controlled experimental tasks regarding speech production or perception, and these tasks may not address the functions of interests in a most natural way (Hasson et al., 2018). Thus, a study investigating the age effects on the semantic processing within a natural context, which includes continuous auditory and natural visual information, (e.g. gestures), could contribute to a more complete picture on this subject.

1.4. Gestures in social communication and aging

Gestures are key elements of social communication. Several studies suggest a positive impact of gestures on communication. The use of gestures contribute to the disambiguation of messages (Holle and Gunter, 2007; Dick et al., 2009), to the organization of information (McNeill, 1992; Goldin-Meadow and Alibali, 2013) and to the retention of the listener's attention (Hostetter, 2011). Moreover, they enhance the performance in memory tasks (Goldin-Meadow et al., 2001; Straube et al., 2009), play an important role in language acquisition and foreign language learning (Goldin-Meadow and Alibali, 2013; Macedonia, 2014) and facilitate the processing of complex speech (Cuevas et al., 2019).

The research of age effects on the interaction of gesture and speech has been principally focused on the production of gestures and used behavioral tasks. The studies were based on groups of participants in advanced adulthood. Cohen and Borsoi (1996) investigated the influence of age on the production of gestures. Their results indicated that older adults, i.e. participants older than 60 years, tended to produce significantly less iconic gestures than younger ones. Similar results regarding the production of deictic, iconic, and metaphoric gestures (also referred as representational gestures) were found by Feyereisen and Havard (1999) considering again adults above 60 years. Özer et al. (2017) explored age-related effects in 50- to 80-years old participants on language production when gestures were restricted/unrestricted. In the unrestricted context, no differences were found regarding the production of gestures, which were mainly beat gestures (also known as non-representational gestures). Finally, Schubotz et al. (2019) examined whether older participants above 60 years adapt language and gestures to the recipients in the same way as younger ones depending on whether the information was known to both participants or not. The results indicate that only younger participants took into consideration if the speech information was shared when conducting the task.

Age-related differences respecting the perception of gestures have received less attention. Montepare et al. (1999) investigated age-related differences concerning the interpretation of emotions expressed by gestures and reported more errors in general produced by participants older than 65 years. Thompson (1995) explored the influence of visible speech and gestures and found that only younger adults benefited from the presentation of gestures, adults older than 64 years profited from visible speech. Thompson and Guzman (1999) described similar conclusions and associated the results to reduced abilities in working memory and reduced inhibition of irrelevant information (mean age elderly group: 76.9). Finally, Cocks et al. (2011) investigated age-related effects on the integration of speech and gesture and showed that adults older than 60 tended to ignore the gesture information when the information provided by the gestures differed from the information provided by the speech.

The available behavioral literature on the influence of age on gesture use and perception is based on advanced adulthood participants. The consideration of middle-aged subjects is important as results revealed from young student samples (He et al., 2018; Kelly et al., 2009a; Kelly et al., 2009b) might not be generalizable to middle or old aged groups, which are -for example- more often investigated in clinical studies (e.g, Cohen and Borsoi, 1996; Feyereisen and Havard, 1999; Özer et al., 2017; Schülke and Straube, 2019). However, despite the evidence about early cognitive decline present in early adulthood, age-related differences regarding the use and perception of gestures within a group of young to middle-aged participants have not been the focus of the analyses.

1.5. Present study

The potential age-related effects on the neural processing of language accompanied by gestures have not been investigated in a natural context. Although some compensatory mechanisms had been proposed concerning the perception of language by older adults, a study examining the perception of semantic complexity measured by the ID in relation to age is lacking. Therefore, the purpose of the current study is to investigate if the age of the subject – already in a young to middle-aged sample – is a relevant factor for the perception of semantically complex passages. Besides, we test whether gestures facilitate the perception of complex passages for the middle-aged adults, or if the additional visual information represents extra effort. First, we hypothesize age-related differences considering that cognitive decline starts already in early adulthood (Park et al., 2002; McNab et al., 2015). This could be signalized by increased activation or by the recruitment of distinct processing strategies during the presentation of complex passages of the story in relation to increasing age. Second, we expect attenuation or disruption of the DMN during the processing of low complexity segments of the story due to the increasing age of the group in comparison to our previous experiment. And finally, we expect a facilitative effect of gestures for middle-aged adults as indicated by a reduced effect of age on complex segments (high > low) when both speech and gesture information is present.

2. Methods

2.1. Participants

A sample of 38 young and middle-aged adults took part in the experiment (21 males and 17 females). The mean age of the participants was 27.05 years (SD = 8.61). All participants were German native speakers. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971), yielding right-handedness in 37 participants. The participants had normal or corrected-to-normal vision and none reported any hearing deficits. For post-hoc analyses this sample has been split based on the median age in a young (19–23 years) and older (24–55 years) participants within early adulthood. None of the participants reported any relevant medical or psychiatric illnesses. All participants gave written informed consent prior to participation in the study. Permission for the study was obtained from the local ethics committee at Philipps University Marburg.

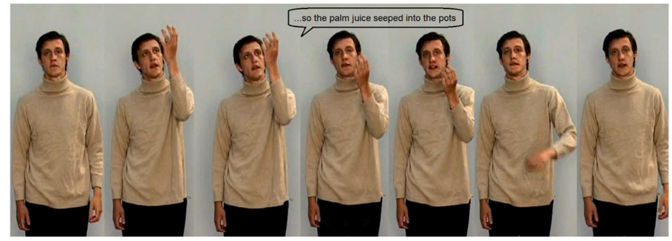

Fig. 1. Example of the stimuli videos. The figure shows seven still frames of the video to illustrate how the actor performed the gestures. A short segment of the story was translated into English and depicted in the speech bubble for illustrative purposes. The actor moved his fingers in the air while moving down his arm indicating how the liquid (palm juice) ran down into the pots. Written informed consent for the publication of this image was obtained from the actor.

2.2. Stimuli

A set of 16 video clips were presented to the participants. The videos displayed an actor narrating consecutive parts of a slightly modified version of the short story "Der Kuli Kimgun" (Dauthendey, 1909). None of the participants knew the story before the experiment. The trained actor of the videos (same actor for all videos) narrated the story as naturally as possible and performed spontaneous gestures of any kind using hands and arms (see Fig. 1). The actor decided freely at which moment and in which way to make the gestures, which were all congruent with the semantic content of the story. The presentation of the videos lasted 32:12 min, with individual clips lasting between 1:02 and 3:31 min. The stimulus material has been already been used in our previous publication (Cuevas et al., 2019).

2.3. Experimental design and procedure

After the acquisition and without interfering with the continuous presentation of the videos, the text of the entire story was divided into segments of ten words each, in order to define segments with low and high ID. A total of 330 segments were defined. Then, the semantic complexity of each segment was measured by the ID. For the complexity analysis, the manual by Chand et al. (2012a) served as an orientation. The guidelines were adapted to the German language taking into consideration the differences between both languages. According to the manual ID values were calculated as follows: counting all propositions in a text, then dividing them by the number of total words, and multiplying the result by ten. Since we chose a segment length of ten words, ID values were directly given by the number of identified ideas within a segment. Each segment of the story had an ID between two and nine (mean = 5.35 SD = 1.12). Between the videos were jitter periods of 6–14 s. The segments that included the end and beginning of a new video encompassed these jitter periods and for this reason were not further analyzed. The number of gestures appearing in each segment was also estimated. All kinds of gestures were included. We expect a general facilitative effect of gesture, as shown by our previous publication (Cuevas et al., 2019). The frequency of the different gesture types did not differ significantly between the low- and high-ID conditions $\chi^2 = 5.19$, $p = .26$). Each segment had between zero and four gestures (mean = 1.50 SD = 0.82). Gestures which happened between two segments were counted in the segment where they started, and in the segment where they ended. Having the ID and gesture value, six different conditions were defined. The segments with an ID value of five or below were counted as low complexity segments and segments which had an ID value of six or higher were considered as high complexity ones. After this segmentation, the low and high segments were divided depending on the number of gestures presented in the segments: zero gestures (low_noG, high_noG), one gesture (low_1G, high_1G), and two or more gestures (low_2 + G, high_2 + G). There was no significant interaction in numbers of trials ($\chi 2 = 3.058$; $p = .214$; frequency: 17 low_ID_noG, 13 high_ID_noG; 91 low_ID_1G; 53 high_ID_1G; 83 low_ID_2G; 73 high_ID_2G) and segment duration ($F(1,324) = 0.410$, $p = .664$, eta-square = 0.003; average duration: 4.46 s low_ID_noG; 5.10 s high_ID_noG; 4.60 s low_ID_1G; 4.87 s high_ID_1G; 4.87 s low_ID_2G; 5.20 s high_ID_2G) between the factors gesture and ID. However, we had fewer trials without gesture and longer duration for the high complexity conditions (main effect complexity; $F(1, 324) = 13.355$, $p < .005$; high: mean = 5.07sec., SD = 1.05; low: 4.71sec., SD = 0.92). This was regarded as unproblematic as our analyses are focused on the interaction between both factors.

For the acquisition of MRI data, the participants were asked to attend to the video and carefully watch and listen to the actor through a mirror mounted on the head coil. Since the participants had no other task than listening and watching, it was possible to investigate the processing of semantic complexity and integration of language and gesture in a natural context. There were several relevant differences from our previous publication regarding the acquisition of the fMRI and behavioral data. First, different headphones were used for the presentation of verbal information (air conduction headphones, Siemens). The loudness of the headphone was kept constant across participants and across sessions. Second, after the experiment, participants were asked whether they liked the story and whether, it was easy for them to follow the story (scale from 1 [not at all] to 7 [yes, very much]). Furthermore, we assessed individual differences regarding gesture sensitivity (Brief Assessment of Gesture scale, BAG, Nagels et al., 2015) to analyze if younger or older adults profited more from the presentation of gestures given their individual sensitivity to gestures. Crystalline intelligence (multiple-choice vocabulary intelligence, MWT-B, Lehrl, 2005) was also measured since it could provide useful information about the influence of vocabulary and intelligence on the perception of narratives.

2.4. fMRI data acquisition

All images were acquired using a 3-T scanner (Siemens MRT Trio series). The functional images were obtained using a T2*-weighted echo-planar image sequence (TR = 2 s, TE = 30 ms, flip angle = 90°, slice thickness = 4 mm, interslice gap = 0.36 mm, field of view = 230 mm, matrix = 64 × 64, voxel size = 3.6 × 3.6 × 4.0 mm, 30 axial slices orientated parallel to the AC-PC line). A total of 970 functional images were acquired (450 during the first run and 520 during the second run). The first run lasted 15 min and the second one 17 min, 20 s due to the varying lengths of individual videos. Simultaneously to fMRI data additional EEG data were acquired. These data were intended to be used for another research project and are will not be further discussed here (He et al., 2018). The use of an EEG cap was not expected to affect the quality of the BOLD responses (Iannetti et al., 2005).

2.5. Data analysis

The MRI images were analyzed using Statistical Parametric Mapping (SPM12; www.fil.ion.ucl.uk) implemented in MATLAB 2009b (Mathworks Inc. Shevorn, MA). The first two volumes were discarded from the analysis to minimize T1-saturation effects. Afterward, all images were registered to the first image of the first run and co-registered to the anatomical volume, normalized into MNI space, and smoothed with an eight mm isotropic gaussian filter. A high-pass filter (cut-off period 128 s) was used. Statistical analysis was performed in a two-level procedure. The design matrix for the modulation of single-subject BOLD responses at the first level comprised the onsets and durations of all six conditions, as well as the six movements parameters of each subject. The hemodynamic response function (HRF) was modeled by the canonical HRF. A flexible factorial second-level analysis with six conditions (NoG_low, 1G_low, 2 + G_low, NoG_high, 1G_high, 2 + G_high) and one covariate including the age of the participants was performed.

A Monte Carlo simulation of the brain volume of the current study was employed to determine an adequate voxel contiguity threshold (Slotnick et al., 2003). It is suggested that this correction provides sensitivity to smaller effect sizes and also corrects for multiple comparisons across the whole brain volume (Slotnick, 2017). Assuming an individual voxel type 1 error of $p < .001$, a cluster extent of 87 contiguous resampled voxels was indicated as necessary to correct for multiple comparisons at $p < .05$. Thus, voxels of clusters with at least 87 voxels and a significance level of $p < .001$ are reported for all contrasts. All described coordinates of activation are located in MNI space. For the anatomical localization of the clusters, the AAL toolbox was employed (Tzourio-Mazoyer et al., 2002).

3. Contrasts of interest

The main focus was on the effect of age on the processing of semantic complexity (effect of the covariate age on the processing of high vs. low complex segments [age × ID interaction]) and its interaction with gestures (effect of the covariate age on the processing of high vs. low complex segments with vs. without gestures [age x ID × gesture interaction]). Besides, the differential contrasts of low_ID > high_ID and high_ID > low_ID and the two contrasts speech > gestures + speech and gestures + speech > speech were also computed to replicate previous findings (Cuevas et al., 2019).

Median split based control analyses, comparing young and older participants in early adulthood were performed to check whether results are influenced by the distribution of the current age range and to facilitate interpretation of the results (for more details and additional control correlation analyses, see supplement material Figs. S3 and S4).

4. Results

4.1. Correlations of age and measures of gesture sensitivity, ratings and MWT-B

At the behavioral level we found no significant effects of age on gesture sensitivity (BAG scores: $r = -0.184$ $p = .269$), post experimental evaluations (whether they liked the story: $r = -0.176$, $p = .291$, measure of crystalline intelligence (MWT-B; $r = 0.316$, $p = .053$), and on whether it was easy for them to follow the story: $r = 0.064$, $p = .704$).

4.2. General fMRI contrasts

Our results replicated some of our previous findings (Cuevas et al., 2019) with a larger and a more heterogeneous sample of participants. Comparing low with high complexity conditions independently of the number of gestures, we observed posterior DMN regions activation during the perception of low complexity passages (see Table 1 and Fig. 2). We found no effect for speech > gestures + speech at our chosen threshold, but with a slightly more liberal cluster size we observed an activation pattern of the left IFG and MTG (see supplemental material, Table S1 and Fig. S1) similar to a previous data set (Cuevas et al., 2019).

4.3. Age-related effects

For the effect of age on the processing of high vs. low complex speech segments, we found activation in left frontal-parietal regions and right angular gyrus (see supplement material, Table S2 and Fig. S2). However, this effect was mainly driven by the segments without gesture as indicated by the significant age x ID × gesture interaction (see Table 1 and Fig. 3). Age correlated especially positively with the BOLD signal during high complexity segments without gestures (see Fig. 3) in the left frontoparietal regions. For segments with gestures this correlation was not significant.

Table 1
Activation peaks and cluster extents.

Contrast	Anatomical region	Cluster extent	Hem.	MNI Coordinates			*F*-value	No. voxels
				x	y	z		
Interaction gesture x complexity x age								
	Middle frontal gyrus	Pars triangularis, superior frontal gyrus	L	−40	54	12	19.36	190
	Middle frontal gyrus	Pars triangularis, superior frontal gyrus, pars opercularis	L	−36	30	32	16.33	148
	Superior parietal gyrus	Inferior parietal gyrus, angular gyrus, middle occipital gyrus	L	−28	−70	50	16.31	224
High complexity > low complexity							**T-value**	
	Middle frontal gyrus	Pars orbitalis, pars triangularis, superior frontal gyrus, insula	R	36	44	2	4.13	167
Low complexity > high complexity								
	Middle temporal gyrus	Supramarginal, angular gyrus, middle occipital gyrus	L	−56	−52	22	5.12	692
	Precuneus	Middle cingulate	L, R	0	−52	48	4.42	386
	Superior temporal gyrus	Middle temporal gyrus, supramarginal, middle occipital gyrus, angular gyrus, superior temporal gyrus	R	64	−48	18	4.33	428

Voxel activations were thresholded at $p < .001$ and only clusters bigger than 87 voxels are reported (montecarlo cluster corrected at $p < .05$). Lateralization of the activation clusters is indicated by L (left) and R (right).

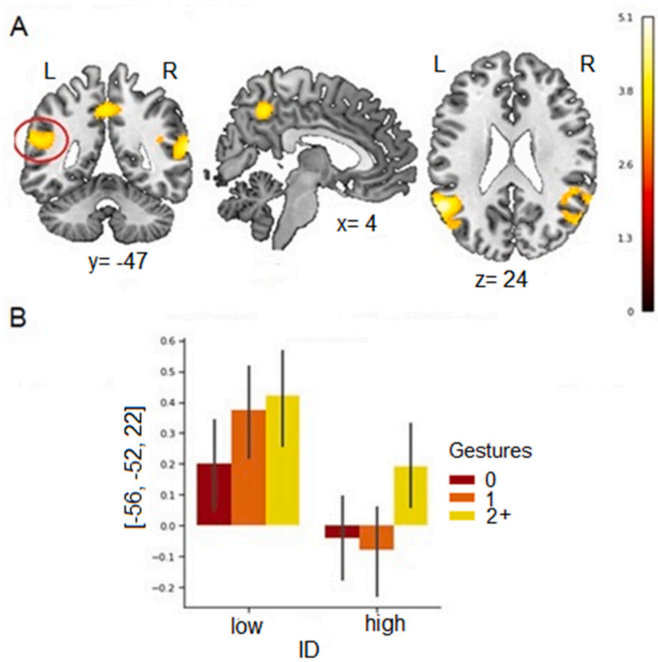

Fig. 2. Activation increase for low complexity. (A) Contrast low ID > high ID. The clusters of activation cover the left middle temporal gyrus, the precuneus, and the right superior temporal gyrus. Panel (B) shows the activation pattern of the cluster localized in the left middle temporal gyrus [-56, −52, 22], highlighted by the red circle in (A), indicating strongest activation during the low complexity conditions. The threshold for voxel activations was set at $p < .001$ uncorr. and only clusters larger than 87 voxels have been included (montecarlo cluster corrected at $p < .05$). Error bars represent standard error of the mean. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.4. Post-hoc fMRI analysis based on median split

We conducted a post-analysis dividing the sample of participants into two groups. The median age was the criterium to make the division. The younger group consisted of the participants younger than 24 years and the older group consisted of participants older than 24 years old (18 vs. 20 participants).

The post-hoc analysis revealed increased activation by subjects older than 24 years for the processing of semantic complexity in comparison to younger subjects (age range 19–23 years) specifically when no gestures were presented (see Fig. 4). This suggests already an early decline in processing of semantic complexity and seems to be a sign of compensation mechanisms recruited by older participants within the early adult lifespan (age range 24–55 years) which are not necessary in a multisensory context (when gestures were presented). See Table S4 in the supplement material for further details.

5. Discussion

In our study, we investigated the neural mechanisms underlying communication and how they are modulated by age. We aimed to clarify how age affects the processing of semantic complexity and gestures in middle-aged participants during the presentation of a continuous narrative story. Overall results corroborated previous findings showing attenuation of DMN with increasing semantic complexity and reduction of activation in language-related areas when speech was accompanied by gestures (Cuevas et al., 2019). Most importantly, we here showed for the first time, that middle-aged adults activated left frontal and parietal regions to larger extents than young subjects during the processing of complex passages that did not contain gestures. Thus, the presentation of gestures reduced the age-related differences for the processing of high complexity semantics passages within these areas. This suggests that gestures might play a facilitative role for older adults, especially when speech is complex.

5.1. Processing of semantic complexity

Our findings regarding the processing of low complexity segments and posterior DMN activation are in accordance with studies investigating age effects on the DMN (Andrews-Hanna et al., 2007; Mevel et al., 2013), who reported anterior-posterior DMN disruption with increasing age. The posterior DMN activation (compared to posterior and anterior activation of DMN regions during the processing of low complexity segments; Cuevas et al., 2019) could be driven by the age-range of the participants (19–55 years), which is larger than in our previous study (22–35 years), where activation in classical DMN regions have been observed. However, findings showing that older adults tend to suppress less DMN (Grady et al., 2006) during a cognitive demanding task is not supported by our results. On the contrary, the contrast high > low complexity conditions revealed increased activation in the right middle frontal gyrus (see Table 1), but not within classical DMN regions. It might be possible that the reduced suppression of DMN is visible in later age stages, since the study conducted by Grady et al. (2006) was based on the data of older adults (20–86 years). Modulation of activation in language-related areas as the MTG and IFG (active especially during the high complexity conditions) was also replicated by our current results (see supplement material, Fig. S1 and Table S1). However, the interaction gestures x complexity could not be replicated as in our previous publication and might be related to the larger variance of age or the use

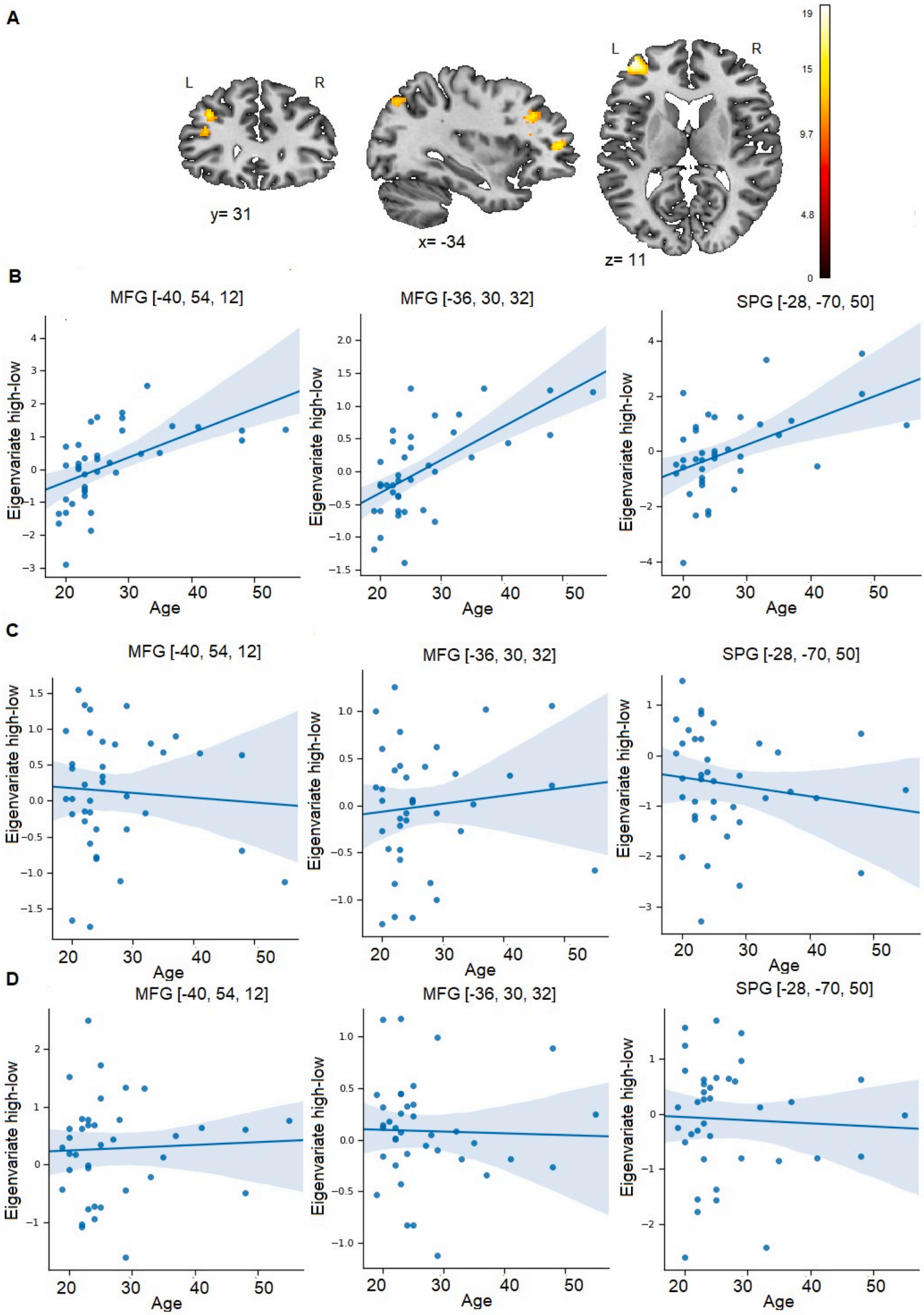

Fig. 3. Interaction analysis of gesture x complexity x age and correlation of BOLD signal with age. (A) Interaction gestures x complexity x age. The clusters of activation cover the left middle frontal gyrus and the left superior parietal gyrus. Panel **(B), (C),** and **(D)** show the difference between the extracted cluster eigenvariate of the high complexity conditions (B: no gesture, C: one gesture, D: two gestures) and the extracted cluster eigenvariate of the three low complexity conditions correlated with the age of the participants. The data was extracted from the three clusters reported in Table 1 (contrast: Interaction gesture x complexity x age). Voxel activations were thresholded at $p < .001$ and only clusters bigger than 87 voxels are reported (montecarlo cluster corrected at $p < .05$). MFG: middle frontal gyrus, SPG: superior parietal gyrus.

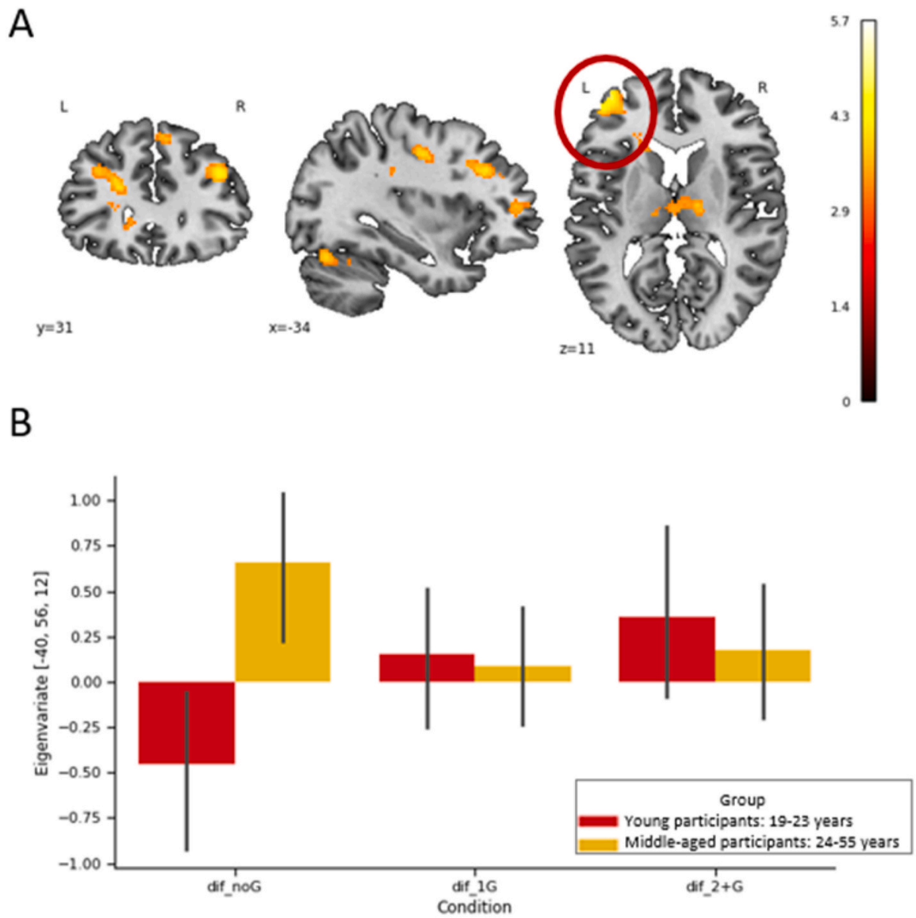

Fig. 4. Post-hoc analysis interaction gestures x complexity x age group. (A) The clusters of activation cover the right angular gyrus, the middle frontal gyrus bilaterally, the caudate, the insula, the precentral gyrus, the cerebellum, and the right superior frontal gyrus. Panel (B) shows the activation pattern of the cluster localized in the left middle frontal gyrus [-40, 56, 12], highlighted by the red circle in (A), indicating strongest activation in the middle-aged group (yellow) during the conditions without gesture information. Voxel activations were thresholded at $p < .001$ uncorr. and only clusters bigger than 87 voxels are included (Monte Carlo cluster corrected at $p < .05$). The error bars represent the standard error of the mean. Dif_noG: high > low ID contrast for no gesture conditions; dif_1G: high > low ID contrast for the one gesture conditions; dif_2 + G: high > low ID contrast for the two or more gestures conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

of different earphones (instead of noise-canceling earphones due to the acquisition of simultaneous EEG-data).

5.2. Age related differences on the processing of speech

Our results are in accordance with previous studies analyzing language decline caused by aging reporting increased activation in frontal and parietal regions in order to accomplish a task. We observed this pattern in the most difficult condition of our experiment: when the complexity is high and no additional information is presented by gestures. Similar results suggesting increased activation in the middle frontal cortex by older participants are reported by Gutchess et al. (2005), who linked the activation of this region to compensation for less activation within the MTG during picture encoding. Concerning the involvement of parietal cortices, similar results are reported by Fera et al. (2005). Bilateral in comparison to unilateral neural responses by younger adults (Cabeza, 2002) are not observed in our current study.

However, the question that arises is, whether this increased activation has a functional character (e.g., due to the increase of semantic complexity) or if the increased activation originates from other aspects of language processing such as word retrieval, processing speed or auditory and visual abilities, or working memory decline. The working memory explanation could be plausible since the compensation was mainly during the most difficult condition where the complexity was high, and no gesture information was available. We suggest that working memory might play a fundamental role in the interpretation of complex passages since participants had to keep in mind the ideas in order to understand the story. Besides, the number of propositions has been proposed as a measure of memory load (Kintsch and Keenan, 1973). Nevertheless, the working memory explanation remains ambiguous since we did not measure working memory capacities directly. Future studies including a sample of adults in advanced adulthood could apply more adequate working memory measures (e.g., as in Schubotz et al., 2020) to test the relationship of working memory capacity and the processing of a continuous narrative. The question if the increased activation is related to the speed of processing is difficult to approach within our model. Given that the participants heard the story at a fixed pace, there is no way to measure whether the older adults needed more time to process the segments. However, the increased activation is present within the duration of the complex segments. Finally, a relevant role of auditory abilities for the increased activation pattern seems rather unlikely. None of the participants reported having any hearing impairment. Moreover, any hearing impairments would also affect the processing of low ID complexity segments, for which we did not observe age-related effects.

On the other hand, word knowledge and general knowledge are usually not affected by age and even have a positive relationship with increasing age (Kemper and Sumner, 2001; Thornton and Light, 2006). Thus, it could be postulated that older adults could show fewer problems with the perception of the story due to richer semantic representations. However, contrary to the findings in the literature, MWT-B scores did not correlate significantly with the age of the participants. It could also be the case that the reduced ability to inhibit irrelevant information in older participants could have played a role in the processing of the narrative (Thompson and Guzman, 1999; Schwarzkopp et al., 2016) since there is evidence that older adults tend to suppress irrelevant information later than younger adults (Schwarzkopp et al., 2016). This latter suppression could lead to increased activation in the frontal and parietal regions. But if this was the case, increased activation during the low complexity condition would also be expected. Given that the compensatory mechanism was specific for the high complexity condition without gesture, a link to inhibitory capacities seems not plausible.

The increased activation in frontotemporal regions could also be explained on the basis of the dedifferentiation theory, which postulates that older adults make use of more diffuse networks (Cabeza, 2002; Park et al., 2004; Meunier et al., 2014). This would suggest that the use of a wider network including parietal regions could be caused by changes in connectivity within the regions which are usually recruited during the perception of complex speech. The use of a less specialized network can also be seen as a sign of less efficiency (Meunier et al., 2014). Thus, it is possible that the older adults activated a wider network during the perception of complex segments. A future study analyzing functional connectivity could provide further insights regarding this issue.

Finally, the increase of activation in frontoparietal regions observed with increasing age could be a specific effect of semantic complexity. The clusters of activation include parts of the inferior frontal cortex, a region, in particular the pars triangularis and the pars opercularis, which is related to the processing syntactic complexity (Stromswold et al., 1996; Caplan et al., 1999). Besides, morphological complexity seems to be related to activation in parietal regions (Schuster et al., 2018). Nevertheless, the measure of ID is independent of sentence length, which is often considered as a sign of syntactic complexity, and sentence structure, since the metric is based on the ideas expressed by ten words and not the words in a sentence. The complexity specific explanation remains however unclear given the insufficient literature about the neural correlates of semantic complexity.

Another relevant factor for the interpretation of the results is the task chosen for our experiment. Especially in age-related experiments approaching language, the type of task or the design of the experiment could influence the results since it is difficult to recognize if the compensatory/increased activation is caused by the task itself or is language-related (Meunier et al., 2014; Shafto and Tyler, 2014). Since our experiment had no explicit task and the speech was uttered within a narrative context, we can assume that the increased activation in the frontoparietal regions with increasing age is more related to language effects and not on task-related effects.

In summary, the age-related differences showed by older/middle-aged adults, namely the increased frontoparietal activation compared to young adults, might be seen as a strategy used to process semantic complex segments of the story. It indicates the dynamic and adaptive qualities of the brain facing a challenging task. This is a pattern typically observed in relation to age, showing middle-aged or older adults' ability to recruit alternative paths or networks to compensate cognitive decline and preserve performance (Cabeza, 2002; Fera et al., 2005; Geerligs et al., 2015). This strategy might be of compensatory nature since it was present during the most cognitive demanding task of the experiment, which is in the context where compensatory strategies are usually recruited (Cabeza et al., 2018). However, this functional mechanism is still not well understood, and working memory decline, reduction of inhibitory abilities as well as structural changes might underline the compensation. Concerning the ID, the increase of activation in the frontoparietal regions by older (24–55 years) compared to younger (19–23 years) adults within the early adult lifespan supports the validity of the metric showing that increasing propositions reflect increasing complexity for the hearer. The results suggest that not only the production of ID (Kemper et al., 2001) but also the perception of ID is affected by age.

5.3. Age-related differences in the perception of gestures

One of the focus of the present study was to investigate if gestures had different effects on the processing of a narrative depending on the age of the participants. Our results differ from the conclusions of previous studies concerning age differences in the processing of co-speech gestures (Thompson, 1995; Thompson and Guzman, 1999; Cocks et al., 2011), probably because our study focused on middle-aged participants while previous studies included participants over the age of seventy. Contradictory to the results by Cocks et al. (2011) who reported that older adults benefited to lesser extents when the information was presented by speech and gestures, our results suggest that middle-aged adults especially benefited from this multimodal coding of information. Gesture presence reduced age-related effects in neural processing. This could be driven by the redundant sending of ideas, namely some ideas were represented in the speech and in the gestures. However, also additional information was sent through the gestures, e.g. the size of an object depicted through the hands of the actor. There are some possible explanations for the differences between our findings and results from previous studies in addition to the differences in the age-range of the participants between the studies. The aforementioned investigations (Thompson, 1995; Thompson and Guzman, 1999; Cocks et al., 2011) used very controlled experiments, where sentences were uttered in isolation, whereas we used naturalistic stimuli in the form of a narrative. Thus, the context of a narrative may influence the perception of language, considering that the utterances have to be integrated into the narrative frame. New and old information could be processed differently within the narrative in comparison to sentences. Furthermore, none of the previous studies analyzed the neural mechanisms involved in the perception of gestures and they only focused on one type of gestures.

As proposed before, the inhibition of irrelevant information could play an important role in the perception of a narrative. If the middle-aged adults had difficulties inhibiting irrelevant information, it could be the case that the presentation of gestures gave a clue to the participants about the relevance of the information uttered. Thus, gestures could have helped with the filtering of relevant/irrelevant information. However, the actor decided freely when to make the gestures and they were not specifically executed during important passages of the story.

The absence of BOLD correlation with age in the gesture conditions could be also indicative of the resilience of the visual cortex during aging (Raz et al., 2004, 2005). It seems that at this stage there are no big differences at the neuronal level concerning the pure perception of movements. Geerligs et al. (2015) reported preserved or even improved connectivity in the visual network. Besides, the sensitivity to gestures seems not to be related to the age of the participants.

In sum, we conclude that, during the comprehension of naturalistic stories, the presentation of multimodal information reduces the processing load of high complexity passages for middle-aged participants. The multimodal encoding of ideas might facilitate their storage in mind, thus improving the interpretation of the narrative.

5.4. Limitations

The term compensation is often described as a strategy, which either reacts to the insufficiency of neural resources to accomplish a task, or leads to a positive effect on performance (Cabeza et al., 2018). Due to the absence of working memory data of the participants, it remains inconclusive if the participants activated the frontoparietal regions to compensate insufficiency in working memory. Nevertheless, our sample is comprised of young and middle age participants, which might differ in neural activation even if they do not differ in behavioral tests from the younger group (Grady et al., 2006). On the other hand, we supposed that the strategy leads to a beneficial effect on the processing, considering that the increased brain activation occurred during the most difficult condition, and that no significant correlation was found between the ability to follow the story and the age of the participants.

6. Conclusion and future research

Age-related differences were found already in early adult lifespan respecting the processing of semantic complexity. The middle-aged adults activated to larger extents frontal and parietal regions during the processing of complex passages, probably as a compensatory mechanism. Second, the simultaneous integration of visual and auditory inputs seems not to be affected by age, at least at this stage. Third, gesture information modulated the age-related differences during the high complex passages, reflecting the facilitative effect of gestures when several propositions are uttered. We conclude that age affects the processing of semantic complexity when the information is not accompanied with visual information. Middle-aged participants profit especially from the multimodal sending of information.

Future experiments could provide complementary insights on this topic. Since age-related effects are visible at this age-range, it would be interesting to conduct a new experiment with a larger sample of participants including older adults and structural measures. It could be investigated if at later age stages different strategies are used in order to achieve cognitive demanding tasks or if the same strategies are used but to bigger extents. Besides, it could be tested if cognitive reserves (measured by episodic memory, attention, language tasks, etc.) have a relation with the increased activation during the processing of complex semantic segments considering that they are associated with efficient processing during high cognitive demands (Bosch et al., 2010).

Credit author statement

P. Cuevas, Conceptualization, Methodology, Validation, Formal analysis, Investigation, Visualization, Writing – original draft, Writing – review & editing, Project administration. Y. He, Validation, Investigation, Resources, Data curation, Writing – review & editing, Funding acquisition. E. Kozasa, Validation, Resources, Writing – review & editing. J. Billino, Validation, Resources, Writing – review & editing. B. Straube, Conceptualization, Methodology, Validation, Writing – review & editing, Supervision, Funding acquisition.

Ethics statement

This study was carried out in accordance with the recommendations of the ethics committee of the medicine faculty of Philipps-University Marburg with written informed consent from all subjects in accordance with the Declaration of Helsinki. The protocol was approved by the ethics committee of the medicine faculty of Philipps-University Marburg.

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Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix ASupplementary data

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