Temporolimbic cortical volume is associated with semantic odor memory performance in aging

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A B S T R A C T

Olfactory function, and specifically semantic olfactory memory (i.e., odor identification), has frequently been shown to predict cognitive functioning across multiple domains in old age. This observation suggests that olfactory function can serve as a marker for the integrity of temporolimbic cortical networks, but a clear delineation of this association is still missing. To address this issue, the present study employed voxel-based morphometry in a region of interest-based design to determine the extent to which gray matter volumes of core olfactory and memory areas are associated with olfactory memory performance in an aging population free from neurodegenerative disease. We further aimed to determine potential overlap in structural anatomical correlates, and differences in association strength, for semantic and episodic olfactory memory. Structural magnetic resonance imaging (MRI), episodic and semantic odor memory and episodic and semantic verbal memory data were collected in 422 participants from the Swedish National Study on Aging and Care in Kungsholmen (SNAC-K), all aged ≥ 60 years. Controlling for age and education, semantic, but not episodic, olfactory memory was positively related to gray matter volume in a cluster extending from the anterior hippocampus and amygdala into the posterior piriform cortex. The observed associations remained even when verbal memory performance was controlled for, supporting a link between the olfactory memory domain and cortical volume over and above more generalized memory abilities. As such, our data provide evidence for distinct functional-structural associations for semantic odor memory, supporting the idea of temporolimbic integrity as a neurobiological substrate linking olfactory function to cognitive health in old age.

1. Introduction

Olfactory impairment is common in the aging population (Murphy et al., 2002), it represents a sensitive predictor for cognitive decline (Doty et al., 1987; Serby et al., 1985; Stanciu et al., 2014), and predicts impending death within a 10-year follow-up interval (Ekström et al., 2017; Pinto et al., 2014; Wilson et al., 2011). Its co-occurrence with known risk factors for damage to the central nervous system (CNS), including genetic risk factors such as APOE 4 and clinical risk factors such as cardiovascular health (Seubert et al., 2017), suggests that subtle changes in the integrity of the CNS are responsible for these associations. However, a clear delineation of the cortical structures linked to olfactory performance in the aging population is still missing.

Most standardized tests of olfactory function that predict health decline tap either directly or indirectly into odor memory abilities. For example, the Sniffin’ Sticks odor identification test, one of the most frequently used diagnostic tests of olfactory dysfunction (Hummel et al., 1997), requires assignment of an object label to a presented odor and, as such, effectively tests semantic memory for odors (Hedner et al., 2010). Other tests, such as odor discrimination, require the ability to hold a working memory representation of one odor and compare it to another. Hence, cortical areas of relevance for olfactory memory processing are of particular interest as potential target regions for explaining the predictive function of olfactory processing for impending health decline. Studies on neural processing of these tasks in healthy young adults (Seubert et al., 2013a), have shed light on unique aspects of cortical olfactory processing that might explain its vulnerability during the early stages of cognitive decline in older individuals. Specifically, functional neural correlates of olfactory stimulation show substantial overlap with medial temporal regions known to be affected in the early stages of dementia (Smitka et al., 2017).
et al., 2012). Direct projections relay olfactory sensory input from the olfactory bulb to the primary olfactory cortex, which, in turn, is tightly linked to limbic and frontotemporal brain areas implicated in memory, executive control, and emotional experience (Landström et al., 2011; Seubert et al., 2013a). This link is thought to give rise to one of the central paradoxes in olfaction where, on the one hand, olfactory memories are long-lasting and intensely emotional (Herz and Schoeller, 2002; Willander and Larsson, 2006), but, on the other hand, difficult to verbalize compared to memories in other sensory modalities (Olofsson and Gottfried, 2015).

This unique feature might explain the sensitivity of olfactory measures for cognitive decline: limited cognitive access makes the use of verbalization compared to memories in other sensory modalities (Olofsson and Gottfried, 2015).

A number of neuroimaging studies have shown a link between gray matter volume in temporal and prefrontal olfactory areas and declarative olfactory memory performance (Frasnelli et al., 2010; Seubert et al., 2013b) as well as with olfactory loss (Bitter et al., 2010b; 2010a; Han et al., 2017). Yet, no study to date has explicitly explored those relationships in a healthy aging population, or investigated whether potential associations extend to areas outside the core olfactory network of piriform cortex, amygdala, and orbitofrontal cortex into supramodal medial temporal lobe structures such as the hippocampus and entorhinal cortex. A closer investigation of such functional-structural relationships in the aging population is needed to determine whether associations between olfactory function and health decline are indeed mediated by temporolimbic network integrity. Furthermore, given the differential neural correlates for semantic and episodic memory (Cabeza and Nyberg, 2000a; Poldrack et al., 2001; Weidemann et al., 2019), the respective neural correlates for different measures of olfactory memory might provide complimentary insights into dissociable subcomponents of impaired odor memory functions, but this has never been directly studied.

Therefore, the present study sought to (a) determine the extent to which gray-matter volumes of core olfactory and memory areas are associated with olfactory memory performance in an aging population free from neurodegenerative disease, and (b) investigate whether these associations persist after controlling for verbal measures of episodic and semantic memory performance to determine whether potential associations are specific to the olfactory modality.

2. Materials and methods

2.1. Participants

Data were derived from the Swedish National Study on Aging and Care in Kungsholmen (SNAC-K), Stockholm, Sweden. SNAC-K uses random sampling stratified by age (60, 66, 72, 78, 81, 84, 87, 90, 93, 96 and 99+ years). At baseline (2001–2004), 3363 (response rate 73.3%) individuals were enrolled in the study and took part in assessment of medical, psychological, and social factors. A subsample of 555 participants underwent an additional magnetic resonance imaging (MRI) assessment.

For the present study, data that did not meet quality assurance criteria due to technical issues during the MRI procedure (n = 6), or suboptimal image quality (n = 46) were excluded from analyses. Additional exclusion criteria were a diagnosis of neurodegenerative disease (n = 5) or epilepsy (n = 1) as well as incidental findings during the MRI evaluation, including evidence of tumors (n = 6), arachnoid cysts (n = 6), ischemia, aneurysms or infarctions (n = 20). Participants who did not complete the olfactory testing portion of the cognitive battery (n = 41) or were over 90 years of age (n = 2) were also excluded. Taken together, the effective sample for the present study consisted of 422 participants (174 males), with a mean age of 70.1 years (SD = 8.7), averaged 12.7 years of education (SD = 4.3). Mini-Mental State Examination (MMSE) scores of the sample ranged from 25 to 30 (mean = 29.13, SD = 1.05).

Assessment of olfactory memory. The episodic and semantic olfactory tasks are described in more detail elsewhere (Larsson et al., 2016). In brief, performance was assessed on the basis of recognition and identification performance on a modified Sniffin’ Sticks 16-item odor identification test (Croy et al., 2015; Hummel et al., 1997). This battery was divided in half to form an encoding set of 8 odors. These were presented to participants, one at a time, with the instruction to memorize each presented odor. The interval between presentations was held constant at 15s. Subsequently, participants were presented with the full set of odors. At odor recognition, participants had to indicate for each odor whether it had been presented before (yes), or was new (no). To index episodic odor memory, number of hits (correct yes answers) and number of false alarms (incorrect yes answers) were recorded. For assessment of semantic memory, participants were first prompted to identify each odor by free identification. If they did not provide a correct answer, they were presented with four written response alternatives, of which they were asked to select the correct one (cued identification). Here, the semantic memory measure reflects the number of correctly identified odors under either the free or the cued response format. To remove the potential impact of perceptual deficits or other reasons for failure to respond, the olfactory memory scores were computed as proportion of correct responses by the number of total pens, where the participant reported perception of an odor. For episodic odor memory, the proportion of false alarms was subtracted from the proportion of hits to account for potential effects of response bias.

Testing occurred in one of three pseudo-randomized orders to avoid sequence effects. In addition, the administration of the olfactory battery within the cognitive test battery varied, with approximately half the group receiving this test in the beginning of their assessment, whereas the remaining participants received it towards the end. Results were averaged across these orders to control for sequence or test-order effects.

Assessment of verbal memory. Verbal semantic memory was measured by a 30-item vocabulary test (Durcan, 1960). Participants identified synonyms for target words out of 5 alternatives and a score of correct identifications synonyms within 7 min was formed. Verbal episodic memory was assessed by means of a word list of 16 unrelated nouns that were both read aloud and presented visually (Laukkka et al., 2013). After the presentation, participants were asked to freely recall as many words as they could remember within 2 min.

2.2. Delineation of regions of interest

The regions of interest were theoretically motivated by inspection of the extant literature to describe regions that represent functionally separate subunits of olfactory and memory networks. They were selected based on the core regions of the olfactory network according to meta-analytical data (Seubert et al., 2013a), and included the anterior and posterior piriform cortex, the olfactory orbitofrontal cortex, the anterior insular cortex, as well as the amygdala and entorhinal cortex. To capture possible effects on more generalized memory functions outside of the core olfactory network, we also included regions of interest for the anterior and posterior hippocampus.

Masks of hippocampus, entorhinal cortex, and amygdala were created on the basis of the Wake Forest University pickatlas toolbox, as implemented in SPM (Maldjian et al., 2003). The hippocampus mask was further divided into an anterior and a posterior part based on recommendations in the literature (Baumann et al., 2010; Becker et al., 2015; Poppenk et al., 2013) to account for possible functional specializations for olfactory memory. Regions of interest (ROIs) were created by segmenting the above-mentioned hippocampal image at the first coronal slice in which the uncus could be clearly observed; voxels anterior to and including this slice were regarded as belonging to the anterior...
hippocampus (AHPC), while voxels posterior to this line were regarded as being part of the posterior hippocampus (PHPC). For the olfactory ROIs, no standardized structural masks are currently available, given the difficulty to define these regions based on macroanatomy or their equivalents in the animal literature (Gonçalves Pereira et al., 2005; Gottfried and Zald, 2005). We therefore used meta-analytical data based on an Activation Likelihood Estimation Analysis of reported activations in 40 individually published olfactory functional MRI studies for the definition of the olfactory orbitofrontal and insular cortices (Seubert et al., 2013a). ROIs were created by transforming the t-map from the meta-analysis into anatomical masks, including all active voxels in the specified regions above a t-value of 50% of that of the local peak voxel (Seubert et al., 2013b). For the piriform cortex, metaanalytical data did not allow for a distinction between the anterior and posterior parts. Given the mounting evidence for a functional relevance of this distinction (Kadohisa and Wilson, 2006; Zelano et al., 2011), separate anatomical masks for the posterior and anterior piriform cortex were used, which were defined by manual delineation of each region in each hemisphere on a separate sample of individual and normalized T1 images from 60 participants (Porada et al., 2019). All binary ROIs were converted into MNI space and multiplied with the binary gray matter mask of our sample. All masks are depicted in Fig. 1. They were combined into one binary mask that was used to restrict the voxel-based morphometry analyses. This mask is available as supplementary material.

MRI data acquisition and analysis. Participants were scanned on a 1.5T MR scanner (Philips Intera, Eindhoven, The Netherlands). The protocol included an axial 3D T1-weighted fast field echo (FFE) [repetition time (TR) 15 ms, echo time (TE) 7 ms, flip angle (FA) 15°, field of view (FOV) 240, 128 slices with a thickness of 1.5 mm and an in-plane resolution 0.94 × 0.94 mm, no gap, matrix 256 × 256].

Olfactory scores were first tested for associations with the key demographic factors of interest: age, education, and sex. The outcome of this analysis determined inclusion as a covariate in the following analysis of structural correlations.

Analysis of the MRI data was performed using SPM12, implemented in Matlab 2014b (Mathworks, Sherborn, MA, United States of America). Images were first bias-corrected and partitioned into different tissue classes using the unified segmentation approach (Ashburner and Friston, 2005). Deformations for image alignment were then estimated by iteratively registering the resulting images with their mean using the DARTEL algorithm (Ashburner, 2007). The resulting template and flow fields were used to create spatially normalized and Jacobian-scaled gray and white matter images in MNI space with a voxel size of 1.5 × 1.5 × 1.5 mm. To account for variations in regional gray matter volume due to differences in brain size between participants, the total intracranial volumes of the subjects were modeled as globals. These globals were then used to scale the preprocessed voxel values to be proportional to the fraction of brain volume accounted for by that particular gray matter voxel using the proportional scaling method within the global normalization function in SPM. As our interest was to compare tissue volumes at different levels of olfactory functioning, we chose to use modulated images, which preserve the total amount of signal from each region. Due to the small volumes of the midbrain/frontotemporal regions of interest, the images were smoothed with a smoothing kernel of 4 mm FWHM to achieve appropriate spatial resolution.

Two separate regression analyses were conducted, predicting local gray matter volume as a function of episodic or semantic olfactory memory score, respectively. Demographic variables were included as covariates if they showed a significant link to olfactory performance at the group level. To determine whether any links between gray matter volume and olfactory performance could be accounted for by memory performance across sensory modalities, analyses were repeated including both semantic and episodic verbal memory scores as additional regressors. The significance level was set to p < .001 uncorrected at peak level, and to a family-wise error-corrected threshold of p < .05 at the cluster level.

Given the lack of prior literature, we complemented the ROI analyses with an exploratory whole-brain analysis to investigate whether any trends for links between memory performance and brain volumes might be observed in areas not covered by the ROI analyses. For this purpose, a global gray-matter binary image was created by thresholding the mean spatially-normalized gray-matter image (computed from all the normalized gray-matter images of the sample) to an absolute value of >0.15, and used as an explicit mask in the regression analyses.

Finally, in any study investigating links between performance measures and brain volume within an aging population with a wide age range, including age as a covariate raises concerns of collinearity between the independent variables. Inspection of variance inflation between odor memory measures, age, and total intracranial volume indicated no concerning effects (all variance inflation factors below 1.2). Another concern could be that any observed effects might be disproportionately influenced by participants with preclinical dementia. To examine this possibility, we re-ran the main analysis excluding participants who were diagnosed with dementia at the follow-up assessment, performed 3–6 years later (n = 23).

2.3. Data and code availability statement

The data and code used in the study are available upon direct request and can be shared or re-used with permission from the authors. These data and code sharing policies comply with the requirements of the funding bodies and the University as well as with institutional ethics approval.

3. Results

Olfactory scores were normally distributed; descriptive statistics of performance and demographic variables, as well as associations between performance measures and associations with demographic variables, are summarized in Table 1.

In brief, both age and education were significantly correlated with episodic and semantic olfactory memory performance and thus entered

![Fig. 1. Regions of interest, overlaid on the mean gray matter image for the sample. Pink: olfactory orbitofrontal cortex, yellow: anterior piriform cortex, red: posterior piriform cortex, green: amygdala, blue: anterior hippocampal gyrus, cyan: posterior hippocampal gyrus, teal: olfactory anterior insula, brown: entorhinal cortex.](image-url)
as covariates in all subsequent analyses. There was no evidence for an effect of sex on olfactory performance within the study sample, and thus, this factor was not further considered in the analyses. Both episodic and semantic verbal memory scores were significantly associated with episodic and semantic olfactory memory. These variables were entered as covariates in the second step of the analyses.

3.1. ROI analyses

Results of the ROI analyses are presented in Table 2 and depicted in Fig. 2. Controlling for age and education, semantic olfactory memory scores were positively associated with gray matter volume in a cluster that peaked in right anterior hippocampus and amygdala and extended into posterior piriform cortex. A symmetrical cluster in the left hemisphere was significant at peak threshold, but failed to meet the threshold for cluster size. No significant associations with performance were found in the insular, orbitofrontal, or entorhinal cortices. This pattern of results remained robust even when the 23 participants with possible pre-clinical dementia were removed from the analysis, indicating that the observed associations were not disproportionately driven by this participant group.

For episodic odor memory, no statistically significant clusters were found; isolated voxels in the AHPC and insular cortex meeting the peak threshold did not meet the threshold for cluster size correction (all k ≤ 15).

Importantly, these effects remained stable even when participants with dementia at follow-up were removed from the analysis.

Multiple regression analyses additionally controlling for semantic and episodic verbal memory yielded a significant positive correlation with verbal episodic memory in the left AHPC; this association did not, however, account for the variance explained by semantic odor memory, which was still observed in the same locations with a slightly larger cluster extent (Table 3). No association to semantic verbal memory was observed.

The exploratory whole brain analyses confirmed the significant effect for semantic odor memory in our region of interest, but did not reveal any clusters outside of the region of interest of sufficient size to survive cluster correction. No effects were found for episodic odor memory. Further details and whole brain t-maps of these analyses for semantic and episodic memory are available as supplementary material.

4. Discussion

The goal of the present study was to delineate correlations between gray matter volume and olfactory memory in a sample of healthy older adults (60–90 years), focusing on cortical areas involved in primary and secondary olfactory sensory processing, as well as temporolimbic memory structures. We further assessed whether these associations were specific to semantic and episodic olfactory memory, that is whether they persisted when verbal measures of episodic and semantic memory performance were controlled for.

Our results demonstrated positive associations between olfactory semantic memory performance and regional gray matter volume in a cluster covering the amygdala, posterior piriform cortex, and anterior hippocampus. No links were found in the remaining parts of the temporolimbic memory network including entorhinal cortex or posterior hippocampus, or in secondary olfactory areas such as the orbitofrontal or anterior insular cortex. Importantly, the associations with gray matter volume remained after controlling for verbal semantic and episodic memory performance, indicating that the observed findings did not reflect a generalized association to memory abilities. On the other hand, no significant correlates of olfactory episodic memory were found, suggesting a less robust link to specific neuroanatomical correlates for this form of olfactory memory.

Our findings can be seen as support for the idea that odor identification, the most commonly used bedside diagnostic test for olfactory function, effectively relies on the integrity of a distinct subset of core temporolimbic structures involved in olfactory, emotional, and memory processing that are often subject to early neural degeneration. Specifically, associations of gray matter volume in anterior parts of hippocampus (AHPC) and odor identification ability are in line with recent work highlighting a functional specialization along its anterior-posterior axis (Poppenk et al., 2013). Although neural connections between piriform cortex and AHPC have not, to our knowledge, been explicitly described in humans, robust connectivity between the AHPC-equivalent ventral hippocampus and piriform cortex has been established in rodents (Poppenk et al., 2013), and linked to olfactory memory (Kesner et al., 2010) as well as to odor detection thresholds (Akrabawi et al., 2016). It is noteworthy that prior studies assessing volumetric correlates of olfactory function in younger adults (Bitter et al., 2010b, 2010a; Frasnelli et al., 2010) have not reported neural correlates of olfactory dysfunction in the hippocampus, but rather, exclusively in primary and secondary olfactory areas. While direct comparisons between older and younger adults are missing, recent evidence indicates that functional connectivity between olfactory and parahippocampal areas may be susceptible to age-related decline in humans (Karunanayaka et al., 2017). As such, our findings raise the possibility of a distinct neural signature of olfactory loss during aging that distinguishes it from impaired olfaction in younger adults. Future studies should determine whether hippocampal neural integrity drives the observed link between olfactory dysfunction and cognitive decline in aging and dementia.

Associations between gray matter volume and olfactory performance were also found in piriform cortex and amygdala, areas that form the basis of odor memory representation (Howard et al., 2009; Wilson and Sullivan, 2011) and are thus thought to play a crucial role in the identification of olfactory stimuli. Most studies examining volumetric
associations of olfactory dysfunction report structural abnormalities in the piriform cortex (Bitter et al., 2010b, 2010a; Frasnelli et al., 2010; Han et al., 2017). While its anterior portion appears to maintain the chemo-topic organizational structure of the olfactory bulb, its posterior portion is thought to encode odors as representations of environmental objects (Gottfried et al., 2006; Howard et al., 2009; Zelano et al., 2011) which are weighted depending on their behavioral relevance (Haberly, 2001). Given that odor identification measures the ability to match an odor sample to an odor object stored in memory, the association with posterior piriform cortex volume found in the present study is well aligned with the previous literature. Results are thresholded at a peak voxel threshold of p < .001 uncorrected and FWE-corrected for cluster size at p < .05. Scatterplot depicts correlation between the gray matter volume at the main peak in the anterior hippocampal cortex and the semantic odor memory score (proportion correct). For the color-region associations, see Fig. 1.

Table 3

Results of ROI analyses for semantic olfactory memory with episodic and semantic verbal memory covariates. Results are thresholded at a peak voxel threshold of p < .001 uncorrected and FWE-corrected for cluster size at p < .05.

| Region          | Hemisphere | Cluster extent | p-peak (unc.) | MNI coordinates |
|-----------------|------------|----------------|---------------|-----------------|
| Olfactory semantic | AHPC       | R              | <.001         | 28 – 9 – 15     |
| Amygdala/PPC    | R          | <.001          | 16 – 8 – 14   |
| Amygdala        | R          | <.001          | 26 – 3 – 27   |
| Verbal Episodic | AHPC       | L              | .001          | –24 – 10 – 33   |

Number of voxels. Notes: AHPC = anterior hippocampal cortex; PPC = Posterior Piriform Cortex, MNI = Montreal Neurological Institute.

Fig. 2. Results of ROI analyses of gray-matter volume associations with semantic odor memory, adjusting for age and education. Results are thresholded at a peak voxel threshold of p < .001 uncorrected and FWE-corrected for cluster size at p < .05. Scatterplot depicts correlation between the gray matter volume at the main peak in the anterior hippocampal cortex and the semantic odor memory score (proportion correct). For the color-region associations, see Fig. 1.
memory retrieval further depends on cognitive subprocesses related to successful short-term storage of the memory representation, as well as the ability to match stored information to new information at retrieval (Cabeza and Nyberg, 2000b). Impairment can thus result from difficulties in basic olfactory, as well as prefrontal and medial temporal functions. Different underlying deficits might therefore result in the same observed response, which would affect our ability to identify robust volumetric correlates.

Links between olfactory memory and cortical gray matter persisted when verbal memory scores were used as covariates. This finding is consistent with the observed behavioral separation of verbal and olfactory memory (Larsson et al., 2016), and further underlines the unique value of olfactory semantic memory as a proxy for neural integrity in temporolimbic cortical networks. Again, odor identification likely depends on a more restricted range of cognitive abilities (template matching) than verbal semantic memory (retrieving semantic associations between different words), and verbal episodic memory (linking a context to a memory). In addition, neural correlates of verbal performance measures are thought to be obscured by the recruitment of compensatory cognitive resources, which maintain performance despite structural losses. Compensation is hereby thought to depend on the available compensatory brain mass (“brain reserve”; Katzman, 1993), and active compensation utilized depending on individual processing style (“cognitive reserve”; Stern, 2009). Given the frequently reported lack of deliberate access to olfactory information (Devanand et al., 2008; MacDonald et al., 2018; Olofsson and Gottfried, 2015), olfactory performance may be less influenced by cognitively driven compensatory mechanisms, resulting in more direct links between gray matter integrity and performance.

Some limitations of this study should be addressed. First, while our data show some notable differences to previous work using younger participant samples, we did not include a young comparison group into the study. Future studies will need to include both old and young participants within the same design to determine whether the observed findings are unique to older individuals, or exacerbated relative to younger individuals.

Further, our functional definitions of primary and secondary olfactory cortex are a snapshot of current knowledge of the functional architecture of the olfactory system. As new data become available (Mazzola et al., 2017), these definitions might be modified.

It is also important to note that cross-sectional design cannot determine whether olfactory memory deficits are a cause or consequence of volumetric loss, or evaluate the clinical relevance of the observed effects. Although we observed reduced olfactory performance with advancing age, it is likely that this presents a mixture of specific aging-related processes, on the one hand, and interpersonal, innate performance differences on the other. Longitudinal studies that monitor participants before and after the onset of measurable cognitive deficits are needed to establish a causal relationship.

Finally, a number of factors may have contributed noise to our data and led to an underestimation of observed effects. While the placement of the olfactory task within a large cohort study enabled us to investigate a relatively large number of subjects, the study design also has some inherent disadvantages. For example, olfactory testing was conducted within the context of a time-consuming larger cognitive battery, as such, we were unable to conduct more extensive olfactory testing, which might have increased the reliability of our behavioral measures. Also, more robust behavioral deficits likely could not be obtained in a study where participants’ main focus lies on assessment of olfactory function. Noise could also stem from the neuroimaging protocol, which was designed to be suitable for investigation of a variety of research questions and was not specifically optimized to capture the areas of interest for this study. Finally, the longitudinal nature of this cohort study means that technical innovations can only be incorporated at a slow pace, with a likely negative impact on data quality compared to more recent cross-sectional studies.

In sum, our data provide evidence that differences in olfactory semantic memory performance, as measured by odor identification, are associated with distinct patterns of differences in regional gray matter volume. The observed correlations map onto key areas implicated in early olfactory processing and memory function, and thereby support the idea of temporolimbic integrity as a neurobiological substrate linking olfactory function to cognitive health in old age. In particular, the link to AHPC volume is of key interest in this regard and should be further explored.

CRediT authorship contribution statement

Janina Seubert: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. Gregoria Kalpouzos: Methodology, Formal analysis, Data curation, Writing - review & editing. Maria Larsson: Conceptualization, Writing - review & editing, Funding acquisition. Thomas Hummel: Writing - review & editing, Funding acquisition. Lars Bäckman: Conceptualization, Resources, Writing - review & editing, Supervision, Funding acquisition. Erika J. Laukka: Conceptualization, Methodology, Formal analysis, Data curation, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuroimage.2020.116600.

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