

Reduced Interhemispheric Transfer in Older Adults: Evidence From a Divided Visual Field One-Back Task

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One of the pivotal structural changes observed in the ageing brain pertains to the corpus callosum, the largest neural pathway interconnecting the two cerebral hemispheres. Studies have highlighted the degeneration of the corpus callosum, particularly in its anterior segments, as individuals age. This prompts an essential question regarding the potential functional repercussions of these structural changes on interhemispheric communication among older adults. Two experiments were conducted to explore potential compromises in the interhemispheric transfer of visual working memory (VWM) in older adults. Both young individuals (aged 18–28 years) and healthy older adults (aged 65–85 years) engaged in modified versions of the one-back paradigm. In this task, stimuli were sequentially presented in either the left or right hemifield, and participants indicated whether each stimulus matched the preceding one. Notably, when two stimuli are matched, they could appear either in the same hemifield or in opposite hemifields. The results revealed that, in comparison to young adults, older adults demonstrated a significant increase in matching errors when the two stimuli were presented in opposite hemifields rather than the same hemifield. This new finding strongly suggests a reduced interhemispheric transfer of VWM in older adults, potentially attributed to age-related atrophy in the anterior part of the corpus callosum.

Public Significance Statement

Younger and older adults performed a memory task where pictures of abstract objects were presented on the left or right side of the display. Older adults commit more memory errors when the objects switch from one side of the display to the other, while this effect was not observed in younger adults. These findings indicate that ageing may be associated with a decline in the ability to transfer information between the two hemispheres of the brain, possibly resulting from deterioration of the corpus callosum.

Keywords: visual working memory, cognitive aging, older adults, interhemispheric transfer

Typical ageing has consistently been linked to cognitive decline across various domains, such as working memory, information processing speed, and executive cognitive function (Murman, 2015). This decline poses a significant challenge to our increasingly ageing societies. Yet, it remains unclear whether this decline in cognitive performance stems from a broad impact on the central nervous system or is rooted in localized structural changes. In that context, the age-related structural degradation of the corpus callosum (CC) emerges as a probable factor. This large white matter structure, which comprised more than 200 million myelinated axonal projections, establishes connections between corresponding cortical regions in the two cerebral hemispheres in an anterior–posterior topographical

arrangement (Aboitiz et al., 1992; Gazzaniga, 2000). Numerous magnetic resonance imaging studies have consistently documented a reduction in both volume and microstructural integrity of the CC in old age (Davis et al., 2009; Delvenne et al., 2021; McLaughlin et al., 2007; Michielse et al., 2010; Ota et al., 2006; Sullivan et al., 2002, 2010). Hence, it is plausible to consider that the general deterioration of the CC could lead to a decline in the integration of sensory-motor and cognitive processes, ultimately resulting in widespread cognitive deterioration.

Although the precise mechanisms remain largely elusive, some evidence suggests a link between decreased cognitive performance and age-related changes in CC structure (Fling et al., 2011; Jokinen et

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al., 2007; Ryberg et al., 2011; Sullivan et al., 2010; Zahr et al., 2009). Even longitudinal data indicate a positive association between CC structural integrity and cognitive performance over time in the context of ageing (Sullivan et al., 2002). However, despite evidence linking the atrophy of the CC in healthy older individuals to general cognitive decline, the specific impact of an ageing CC on inter-hemispheric communication remains uncertain. Given the correlation between CC size and the quantity of myelinated and nonmyelinated transcallosal fibers required for transmitting neuronal impulses between hemispheres (Aboitiz et al., 1992), it is plausible to propose that interhemispheric communication may experience some disruption in older age compared to younger adulthood.

Previous research investigating the impact of ageing on inter-hemispheric communication has primarily employed assessments of visuomotor interhemispheric transfer time (IHTT) through the utilization of the Poffenberger paradigm (Poffenberger, 1912). The paradigm examines variations in reaction times (RTs) by analyzing the interhemispheric (crossed, e.g., left hemisphere/right hand) and intrahemispheric (uncrossed, e.g., left hemisphere/left hand) response pathways, referred to as the crossed–uncrossed difference (CUD). Numerous studies have noted a lengthening of IHTT in older adults (Bellis & Wilber, 2001; Davis et al., 2012; Jeeves & Moes, 1996; Reuter-Lorenz & Stanczak, 2000), although some studies have failed to observe any ageing effects (Linnet & Roser, 2012). Evidence suggests that the CUD may rely on transfer through anterior CC regions, such as the CC midbody or genu (Gawryluk et al., 2011; Omura et al., 2004; Tettamanti et al., 2002; Weber et al., 2005). The potential reliance of the CUD on anterior interhemispheric pathways, along with the age-related degradation of the CC, could explain the documented elevation of CUD in older adults.

Although a prolonged IHTT is a clear indicator of an age-related disruption in interhemispheric communication, the question remains as to whether higher cognitive processes reliant on such communication are also disrupted in old age. One study has recently examined this question by assessing the ability of one hemisphere to inhibit information from the other. Delvenne and Castronovo (2018) used a divided-field Stroop paradigm wherein the target and distracter were spatially separated and presented either both within a single hemifield or each in a different hemifield. The study revealed that young adults exhibited consistent Stroop interference levels, irrespective of whether the target and distracter were presented unilaterally or bilaterally. This implies that a fully developed and healthy CC inherently facilitates information exchange between hemispheres, even though such transmission may negatively impact task performance. Conversely, older participants exhibited a noteworthy reduction in interhemispheric interference compared to intrahemispheric interference, suggesting a partial disruption in the automatic nature of interhemispheric transfer. Therefore, emerging research suggests that interhemispheric communication undergoes disruption in old age, potentially influencing higher cognitive processes, including inhibition processing. However, additional research is clearly required to explore further the functional implications of age-related CC degeneration across various cognitive domains.

In the present study, we investigated potential age-related differences in interhemispheric communication in the context of visual working memory (VWM), the ability to temporarily process and maintain visual information. Similarly to the contralateral organization of visual processing, research has shown that the representations in VWM are, at least to some extent, stored in the

hemisphere contralateral to the hemifield in which the information is displayed (Delvenne, 2012; Delvenne et al., 2011; Gratton, 1998; Gratton et al., 1997; Vogel & Machizawa, 2004). The memory traces are then integrated and exchanged across the two hemispheres through the CC (Brincat et al., 2021; Gazzaniga, 2000). In the event of a partial disruption in interhemispheric communication among older individuals, the visual information processed and temporarily stored by one hemisphere might not be exchanged as efficiently with the other hemisphere, unlike in younger adults. In simpler terms, there is a reasonable assumption that older adults could exhibit a more pronounced decline in VWM when the memory and test arrays are presented in opposite hemifields.

To the best of my knowledge, the ability to integrate memory traces across hemifields/hemispheres in older adults has not yet been investigated. In the present study, two experiments using an adaptation of the well-known *N*-back paradigm were carried out. In a typical *N*-back task, participants are presented with a sequence of individual stimuli and must indicate whether the stimulus presented matches the stimulus presented *N* items before. This task was originally developed by Kirchner (1958) and has been extensively used as a measure of working memory. Here, we implemented a hemifield manipulation in the visual one-back task, which involved the stimuli being presented in either the left or right hemifield. Consequently, the two matching stimuli could appear in the same hemifield (e.g., both in the left hemifield) or in opposite hemifields (e.g., the first stimulus in the left hemifield and the second in the right hemifield). When presented in opposite hemifields, effective matching requires interhemispheric communication, as these VWM traces are encoded and stored separately across the left and right hemispheres (e.g., Gratton et al., 1997). If there is a reduction in VWM interhemispheric transfer in older adults, a more pronounced decline in their VWM performance may be observed when the matching stimuli are presented in opposite hemifields compared to when they are in the same hemifield.

Transparency and Openness

The experimental protocol was approved by the School of Psychology Research Ethics Committee, from the University of Leeds (title of the project: “The Effect of Ageing on Visual Working Memory Within and Across Hemifields”; Approval Reference Number: PSYC-126). Participants were treated in accordance with the Declaration of Helsinki. The study design, hypotheses, and analysis plan were not preregistered. The Method section reports how the sample size was determined, any data exclusions, all manipulations, and all measures. De-identified data and materials are available on the Open Science Framework at https://osf.io/5qfpu/?view_only=9d026bf5daaa41a48739cd525fb890cb. Analytic code was not provided for findings that can straightforwardly be reproduced using analyses of variance (ANOVAs). Data were analyzed using SPSS Statistics (Version 29).

Experiment 1

Method

Participants

Based on an a priori power calculation with G*Power (Version 3.1.9), a total sample size of 54 participants was recommended. This

is to detect a small effect ($f = 0.25$) for a repeated measures ANOVA with within-between interaction between the two groups (young and older adults) and measurements (same and different hemifields) and would result in an actual power of 0.950. According to the sample size calculations, it was recommended to recruit a minimum of 27 participants per age group; however, due to the study being carried out online, a higher sample size was aimed for.

We tested 38 young adults (32 females) aged 18–22 ($M_{\text{age}} = 18.74$; $SD = 0.76$) and 38 older adults (16 females) aged 65–85 ($M_{\text{age}} = 68.92$; $SD = 4.06$). The racial distributions of the samples were not recorded, and all participants resided in the United Kingdom. Young participants were recruited using the Participant Pool Scheme from the University of Leeds Psychology Department and the online recruitment platform Prolific (<https://www.prolific.co>). Those recruited from the Participant Pool Scheme received course credits, and those recruited through Prolific received £5 for participating. Older participants were recruited using Prolific and were screened for possible underlying neurological disturbances with the Mini Montreal Cognitive Assessment (Mini MoCA; Nasreddine et al., 2005). The MoCA has been found to have high construct validity (Freitas et al., 2011) and higher diagnostic reliability compared to a similar well-known cognitive impairment screening test, the minimal state examination (Folstein et al., 1975). The recommended cutoff score of 11 was applied, and all the older adults recruited here achieved at least that score. All participants were monolingual (self-reported) and right-handed, as determined by a score of at least +50 on an online version of the Edinburgh Handedness questionnaire (Oldfield, 1971). They also self-reported no history of neurological problems, correct color vision, and normal or corrected-to-normal visual acuity.

Apparatus and Stimuli

The stimuli were displayed on the participants' computer screens, and the experiment was run using the online research platform Gorilla (<https://www.gorilla.sc>). The stimuli were distorted versions of the revised set of Snodgrass and Vanderwart's (1980) object databank (Rossion & Pourtois, 2004) and appeared abstract and meaningless (see McKeown et al., 2014 and Figure 1). The size of

each stimulus was 150×150 pixels. The stimuli were presented laterally at the center of the left or right half of the computer screen against a white background.

Design and Procedure

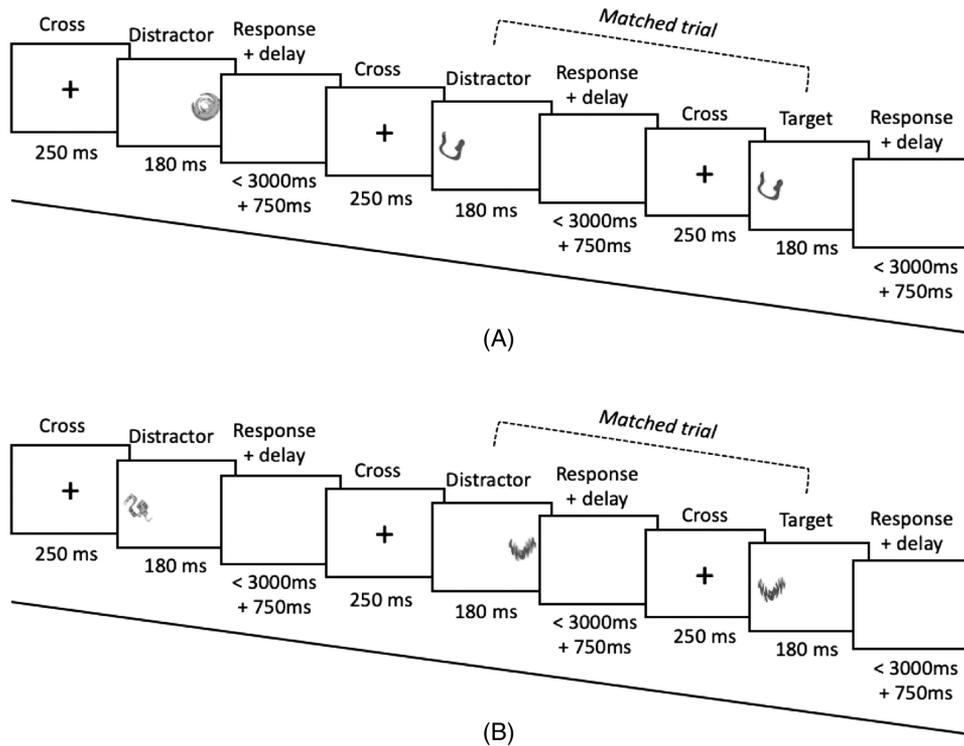
Data collection started in January 2020 and was completed in April 2020. Participants were provided with a URL link to initiate the experiment. No constraints were implemented to require the usage of specific equipment, except that the experiment could only be conducted on a desktop computer or laptop and was not compatible with tablets or phones. Instructions were shown on the screen, followed up by a consent form that participants had to tick to indicate they agreed to partake in the study. Participants then completed the Edinburgh Handedness questionnaire, the mini MoCA, and finally, the main experimental one-back task. The study employed a mixed two-way (2×2) design with group (young adults vs. older adults) acting as the between-subjects independent variable and display (same-hemifield vs. different-hemifield) as the within-subjects independent variable. Although the main dependent variable was the accuracy score calculated as the percentage of correct responses, reaction times were also recorded. As shown in Figure 2, each trial of the main experimental task started with the presentation of a central black fixation cross at the center of the screen for 250 ms. Participants were encouraged, through instructions, to fixate on the center of the screen. One stimulus was then presented, either on the left or right side of the screen, for 180 ms, a presentation time commonly considered short enough to prevent saccadic eye movements (Bourne, 2006; Carpenter, 1988). From the occurrence of a second stimulus onward, participants were instructed to decide as quickly as possible whether the stimulus matched the one that immediately preceded it. Responses had to be made within 3,000 ms of the onset of the stimulus by pressing the appropriate key on the computer keyboard ("k" = same; "d" = different). The next trial began 750 ms after a response had been made or after 3,750 ms if no response had been recorded.

Out of the 260 stimuli available, 204 stimuli were randomly selected and never repeated throughout the study. The experiment consisted of a training block of 12 trials and six experimental blocks of 32 trials each. Within each block of experimental trials, a stimulus matched the immediately preceding one on eight occasions, meaning that within each block, there were eight matched trials and 24 nonmatched trials. Matched and nonmatched trials were randomly presented within each block. Including fewer matched trials compared to nonmatched trials may not only decrease the probability of guessing but could also incentivize participants to sustain focused attention on the task, as the omission of a matched trial would carry a higher cost. The location (i.e., left or right) of the stimuli on the screen was also randomly displayed with the constraint that half of the matched trials shared the same hemifield (i.e., same-hemifield condition) and the other half were displayed in opposite hemifields (i.e., different-hemifield condition). This resulted in a total of 48 matched trials per participant, with 24 trials in the same-hemifield condition and 24 trials in the different-hemifield condition, and 144 unmatched trials, with 72 trials in the same-hemifield condition and 72 trials in the different-hemifield condition. The complete task, including the mini MoCA, handedness questionnaire, etc., lasted approximately 40 min.

Figure 1
Examples of the Stimuli Used in This Study



Figure 2
Illustrations of the Different Conditions Used in Experiment 1



Note. (A) Example of a matched trial in the same-hemifield condition. (B) Example of a matched trial in the different-hemifield condition. The stimuli are not drawn to scale for illustration purposes. The symbol “+” represents “cross” in the figure.

Results

Even though accuracy was the primary dependent measure as the study was conducted online and there was no explicit request for speedy responses, mixed-design ANOVAs on RTs, with display (same-hemifield vs. different hemifield) as the within-subjects variable, and group (young vs. older adults) as the between-subjects variable, were first conducted. The mixed-design ANOVA on correctly matched trials revealed no significant effects. The mixed-design ANOVA on correct unmatched trials revealed a marginal effect of group, $F(1, 74) = 3.86, p = .053$, partial $\eta^2 = .050$, with older adults ($M = 939$ ms, $SD = 229$) being slightly slower than young adults ($M = 845$ ms, $SD = 202$). There was a significant effect of Display, $F(1, 74) = 10.74, p = .002$, partial $\eta^2 = .127$, with slower responses in the different-hemifield condition ($M = 914$ ms, $SD = 247$) as compared to the same-hemifield condition ($M = 870$ ms, $SD = 189$). No other effects were found.

The mixed-design ANOVA on the percentage of correct responses for the matched trials revealed a significant effect of group, $F(1, 74) = 9.33, p = .003$, partial $\eta^2 = .112$, with higher accuracy in young adults ($M = 81.62$, $SD = 16.49$) as compared to older adults ($M = 71.27$, $SD = 20.96$). The effect of Display was not significant ($p = .153$), suggesting similar overall performance in the same-hemifield and different-hemifield conditions. Interestingly, as it can be seen clearly in Figure 3A, the Display \times Group interaction was significant, $F(1, 74) = 6.57, p = .012$, partial $\eta^2 = .082$, showing an effect of Display only for older adults, $t(37) = 2.56, p = .015$, but not for young adults

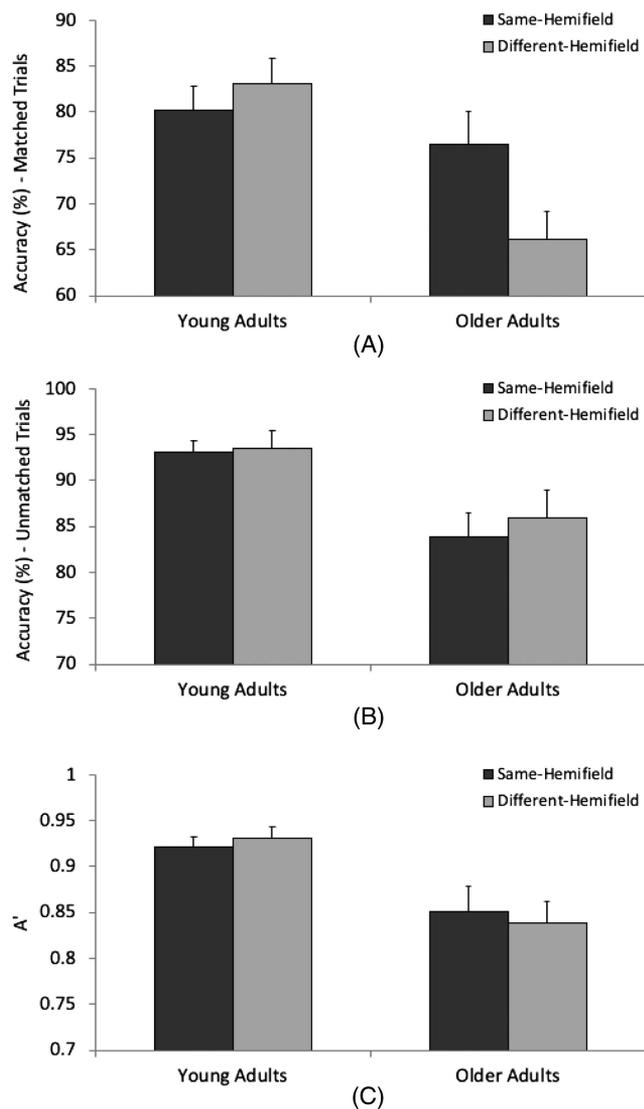
($p = .374$). The effect of Display in older adults revealed lower accuracy in the different-hemifield condition ($M = 66.08$, $SD = 18.88$) as compared to the same-hemifield condition ($M = 76.46$, $SD = 21.88$). The Display \times Group interaction also showed a significant group effect in the different-hemifield condition, $t(74) = 4.15, p < .001$, where young adults ($M = 83.07$, $SD = 16.74$) performed better than older adults ($M = 66.09$, $SD = 18.88$). In contrast, no group effect was found in the same-hemifield condition ($p = .405$).

The mixed-design ANOVA on the percentage of correct responses for the unmatched trials (Figure 3B) revealed a significant effect of group, $F(1, 74) = 7.84, p = .007$, partial $\eta^2 = .096$, with higher accuracy in young adults ($M = 93.28$, $SD = 9.61$) as compared to older adults ($M = 84.86$, $SD = 17.34$). No other effects were found.

Finally, analyses were conducted on the measure of sensitivity A' (Figure 3C). The mixed-design ANOVA on A' revealed a significant effect of group, $F(1, 74) = 9.81, p = .002$, partial $\eta^2 = .117$, with higher A' values in young adults ($M = 0.93$, $SD = 0.08$) as compared to older adults ($M = 0.85$, $SD = 0.15$). No other effects were found.

¹ A' increases from 0.5 for chance performance to 1.0 for perfect performance (Macmillan & Creelman, 2005). A' was calculated following the formula developed by Grier (1971): $A' = 0.5 + [(H - g)(1 + H - g) / 4H(1 - g)]$, where H is the rate of correct detection (Hit Rate—namely the matched trials), and g is the rate of incorrect detection (guessing rate). When g was greater than H , the following formula was used (Aaronson & Watts, 1987): $A' = 0.5 - [(g - H)(1 + g - H) / 4g(1 - H)]$.

Figure 3
Results of Experiment 1



Note. Error bars represent standard errors of the mean values.

In summary, the findings indicated a significant decline in VWM performance among older adults compared to younger individuals. This decline was evident across both matched and unmatched trials, as well as in the measure of sensitivity A' . Furthermore, older adults exhibited a notable reduction in VWM performance when matching stimuli were presented in opposite hemifields compared to the same hemifield, suggesting a potential disruption in interhemispheric communication. However, this effect was not found when sensitivity measures were considered, which hinders definitive conclusions at this point.

Experiment 2

In the first experiment, when matching stimuli were presented in different hemifields, they naturally occupied distinct locations. In contrast, in the same-hemifield condition, the matching stimuli

shared the exact same location. This raises the possibility that older adults may be more influenced by a change in location between the memory and test stimuli rather than solely by a change of hemifield. This could be particularly significant if older adults encounter difficulties in shifting attention between different locations or in transferring information from iconic memory, the brief sensory memory system that holds visual information for a fraction of a second, to working memory. When the two matching stimuli are presented at the same location, performance might rely on residuals of iconic memory without necessitating the transfer of these sensory representations into VWM. Despite the time between two matching stimuli (i.e., approximately 1950 ms, which includes an average response time of 954 ms in older adults, a fixed delay of 750 ms, and a 250 ms fixation cross) surpassing the duration of iconic memory (Sperling, 1960), and the likelihood of the fixation cross acting as a visual mask that disrupts iconic memory, a second experiment was conducted to explicitly eliminate this possibility.

Method

Participants

Because this second experiment used the same number of trials and variables as in the first experiment, the same a priori power calculation was used with a recommended total sample size of at least 54 participants. We tested 37 new young adults (25 females) aged 18–28 ($M_{age} = 21.19$; $SD = 2.51$) and 37 new older adults (19 females) aged 65–74 ($M_{age} = 68.32$; $SD = 2.73$). The racial distributions of the samples were not recorded, and all participants resided in the United Kingdom. Participants were recruited and screened in the same way as for Experiment 1. All older adults passed the mini MoCA, and all participants self-reported being monolingual, having correct color vision and normal or corrected-to-normal visual acuity, and no history of neurological problems. They were also right-handed, as determined by a score of at least +50 on the Edinburgh Handedness questionnaire.

Stimuli and Procedure

Participants completed the same one-back task as in Experiment 1. However, the following changes were made: the stimuli were presented laterally at both the center of the left half or right half of the computer screen and the center of the top half or bottom half of the screen. As a result, the stimuli were presented at four different locations on the screen: top left, bottom left, top right, or bottom right. The location of the stimuli on the screen was randomly displayed with the constraint that half of the matched trials shared the same hemifield but not the same location (e.g., one stimulus at the bottom-left and the matching stimulus at the top-left) and the other half of the matched trials were displayed in opposite hemifields (e.g., one stimulus at the bottom-left and the matching stimulus at the bottom-right; see Figure 4). The number of trials and all the other parameters of the experiment were identical to Experiment 1.

Results

Regarding the RTs, the mixed-design ANOVA on the correct matched trials revealed a significant effect of group, $F(1, 72) = 4.99$, $p = .029$, partial $\eta^2 = .065$, with older adults ($M = 821$ ms,

$SD = 242$) being slower than young adults ($M = 715$ ms, $SD = 167$). No other effects were found. The analyses on the correct unmatched trials revealed a significant effect of group, $F(1, 72) = 8.05, p = .006$, partial $\eta^2 = .101$, with older adults ($M = 829$ ms, $SD = 216$) being slower than young adults ($M = 700$ ms, $SD = 176$). No other effects were found.

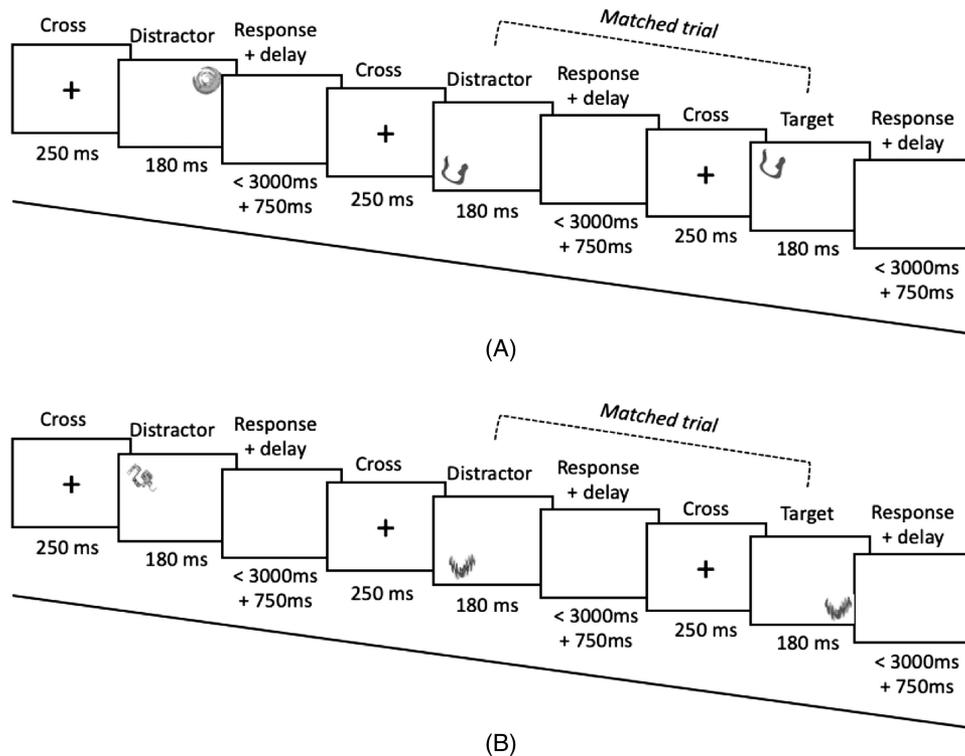
For accuracy, the mixed-design ANOVA on the percentage of correct responses for the matched trials (Figure 5A) revealed a significant effect of group, $F(1, 72) = 4.29, p = .042$, partial $\eta^2 = .056$, with higher accuracy in young adults ($M = 77.7, SD = 13$) as compared to older adults ($M = 70.8, SD = 17.35$). The effect of Display was significant, $F(1, 72) = 12.65, p < .001$, partial $\eta^2 = .149$, with better accuracy in the same-hemifield condition ($M = 76.33, SD = 14.64$) than in the different-hemifield condition ($M = 72.12, SD = 16.46$). Similarly to Experiment 1, the Display \times Group interaction was also significant, $F(1, 72) = 4.03, p < .05$, partial $\eta^2 = .053$, showing better accuracy in the same-hemifield condition ($M = 86.22, SD = 13.87$) than in the different-hemifield condition ($M = 82.68, SD = 16.19$) for older adults, $t(36) = 4.00, p < .001$, but not for young adults ($p = .288$). The Display \times Group interaction also showed a significant group effect in the different-hemifield condition, $t(72) = 2.53, p = .014$, where young adults ($M = 76.74, SD = 13.59$)

performed better than older adults ($M = 67.36, SD = 17.97$). In contrast, no group effect was found in the same-hemifield condition ($p = .195$).

The mixed-design ANOVA on the percentage of correct responses for the unmatched trials (Figure 5B) did not reveal any significant effects.

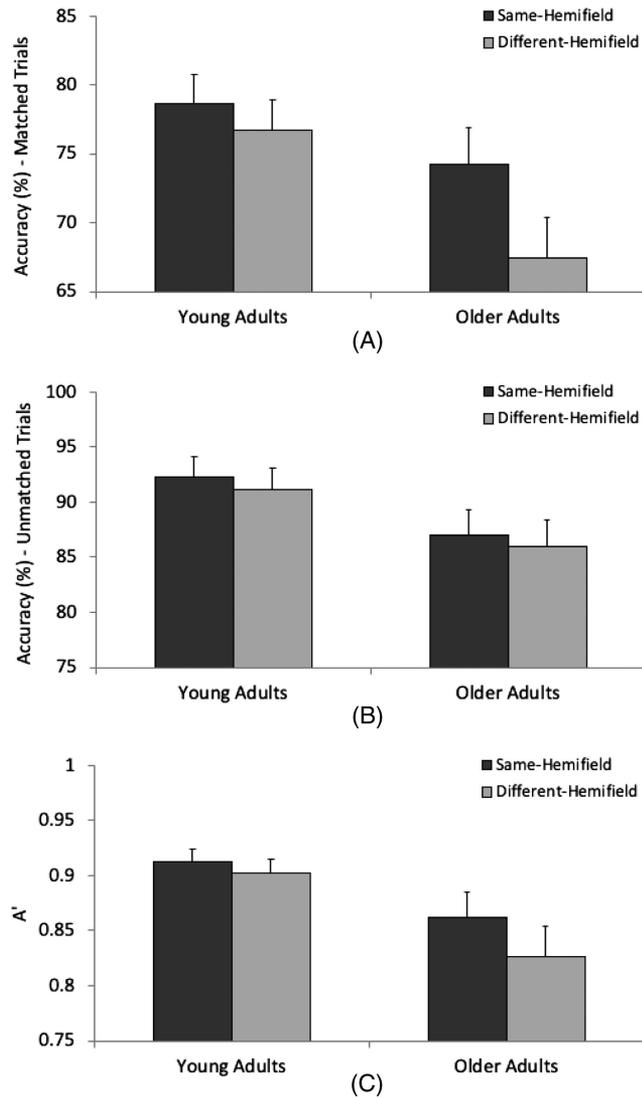
The analyses on A' (Figure 5C) revealed a significant effect of group, $F(1, 72) = 5.45, p = .022$, partial $\eta^2 = .070$, with higher A' values in young adults ($M = 0.91, SD = 0.07$) as compared to older adults ($M = 0.84, SD = 0.15$). The effect of Display was significant, $F(1, 72) = 16.88, p < .001$, partial $\eta^2 = .190$, with higher A' values in the same-hemifield condition ($M = 0.89, SD = 0.11$) than in the different-hemifield condition ($M = 0.86, SD = 0.13$). The Display \times Group interaction was also significant, $F(1, 72) = 5.48, p = .022$, partial $\eta^2 = .071$, showing a significant difference in A' values between the same-hemifield condition ($M = 0.86, SD = 0.14$) and the different-hemifield condition ($M = 0.83, SD = 0.16$) for older adults, $t(36) = 3.88, p < .001$, but not for young adults ($p = .122$). The Display \times Group interaction also showed a significant difference in A' values between young adults ($M = 0.90, SD = 0.07$) and older adults ($M = 0.83, SD = 0.16$) in the different-hemifield condition, $t(51) = 2.59, p = .013$, but not in the same-hemifield condition ($p = .056$).

Figure 4
Illustrations of the Different Conditions Used in Experiment 2



Note. (A) Example of a matched trial in the same-hemifield condition. (B) Example of a matched trial in the different-hemifield condition. The stimuli are not drawn to scale for illustration purposes. The symbol “+” represents “cross” in the figure.

Figure 5
Results of Experiment 2



Note. Error bars represent standard errors of the mean values.

In summary, the findings from this second experiment further underscored the significant decline in VWM performance observed among older adults compared to their younger counterparts. Compared to younger participants, older adults not only exhibited slower response times for both matched and unmatched trials but also demonstrated lower accuracy in matched trials and reduced scores in sensitivity data. Consistent with Experiment 1, older adults also showed a distinct decline in VWM performance when matching stimuli were presented in opposite hemifields compared to the same hemifield. However, unlike Experiment 1, this effect was also corroborated by lower A' values in the different-hemifield condition compared to the same-hemifield condition among older adults. Additionally, the results from this second experiment suggest that this effect cannot be solely attributed to changes in stimulus location or performance influenced by iconic memory residuals. Instead, they

compellingly indicate a decline in interhemispheric communication within VWM associated with ageing.

General Discussion

The primary objective of this study was to examine how typical ageing affects interhemispheric communication in the context of VWM. Previous research has predominantly explored the relationship between age-related CC degeneration and interhemispheric communication, primarily using visuomotor IHTT assessments. However, the specific impact of ageing on higher cognitive processes relying on interhemispheric communication has received less attention (Delvenne & Castronovo, 2018). To investigate this, a divided-field one-back paradigm was used, exploring the influence of ageing on the ability to transfer visual memory traces between hemispheres by presenting visual stimuli in either the left or right hemifield. Given the contralateral organization of visual memories (Delvenne, 2012; Delvenne et al., 2011; Gratton, 1998; Gratton et al., 1997; Vogel & Machizawa, 2004), where the two hemispheres need to communicate for accurate matching of bilateral stimuli, the present study aimed to uncover age-related effects on this process.

The results revealed that young adults maintained consistent VWM performance regardless of whether stimuli appeared in the same or opposite hemifields. This suggests that a fully developed and healthy CC facilitates the exchange of memory traces between hemispheres without additional cost. In contrast, older participants showed a notable decrease in VWM performance when matching stimuli were presented in opposite hemifields compared to the same hemifield, indicating a potential disruption in interhemispheric communication. It is crucial to note that this decline in performance among older adults was not simply due to speed-accuracy trade-offs, as their reduced performance was not associated with shorter reaction times. This effect was confirmed by sensitivity analysis in the second experiment, revealing lower sensitivity in older adults for between-hemifield trials compared to same-hemifield trials. Although it is not clear why the sensitivity analysis did not confirm the effect in Experiment 1, Experiment 2 provided a clearer picture as it eliminated factors such as a mere change in stimulus location or reliance on iconic memory residuals. This strengthens the argument that the observed decline in VWM performance in this study is, at least partially, linked to disrupted interhemispheric communication associated with ageing.

Given the degenerative process observed in the CC of older adults (Aboitiz et al., 1992; Burke & Yeo, 1994; Davis et al., 2009; Hou & Pakkenberg, 2012; McLaughlin et al., 2007; Michielse et al., 2010; Ota et al., 2006; Sullivan et al., 2002, 2010), it is reasonable to suggest that the reduced interhemispheric transfer of VWM traces may directly result from callosal atrophy associated with typical ageing. This assertion aligns with recent findings from a Diffusion Tensor Imaging study (Qin et al., 2016), which indicated a positive relationship between the integrity of the posterior CC and the occurrence of opposite hemifield illusory conjunctions in a VWM task. Specifically, individuals with greater posterior CC integrity exhibited more bilateral illusory conjunctions, implying stronger interhemispheric transfer. The findings also align with existing literature on age-related differences in interhemispheric transfer relying on the anterior section of the CC, which connects bilateral frontal cortex areas (Gawryluk et al., 2011; Omura et al., 2004; Tettamanti et al., 2002; Weber et al., 2005). Although recent findings

have shown that specific tracts of the posterior CC, namely temporal and parietal tracts, have lower matter integrity in typical aging (Delvenne et al., 2021), the age-related CC atrophy seems to follow a gradient of decline from anterior to posterior (Lebel et al., 2012). Specifically, the typical ageing process appears to predominantly impact the small-diameter commissural tracts of the anterior CC section, referred to as the genu, projecting to bilateral areas of the frontal cortex (Bastin et al., 2008; Davis et al., 2009; Fan et al., 2019; Hou & Pakkenberg, 2012; Salat et al., 2005; Schulte et al., 2005; Sullivan et al., 2010). This pattern aligns with age-related cognitive decline observed in functions localized in the frontal regions, such as task switching (Wasylyshyn et al., 2011), declarative memory (Rosen et al., 2002), problem solving (Zahr et al., 2009), processing speed, and working memory (Fling et al., 2011; Madden et al., 2009; Milham et al., 2002; Reuter-Lorenz, 2002). Given that the frontal, and especially the prefrontal, cortex plays a crucial role in VWM (Goldman-Rakic, 2011; Miller, 2000; Miller & Cohen, 2001; Owen et al., 2005), the age-related atrophy of the anterior part of the CC appears to be a plausible explanation for the observed decline in the interhemispheric transfer of VWM traces, affecting both basic visuomotor interhemispheric transfer (Bellis & Wilber, 2001; Davis et al., 2012; Jeeves & Moes, 1996; Reuter-Lorenz & Stanczak, 2000) and higher cognitive processes dependent on such communication (Delvenne & Castronovo, 2018).

However, the cross-sectional design of the study limits the ability to establish firm causation or understand the trajectory of age-related differences. Future longitudinal studies could provide a more comprehensible understanding of CC degeneration and its impact on interhemispheric transfer, including the transfer of VWM. Moreover, the study did not delve into the neural mechanisms underlying the observed effects. A more direct link between the integrity of the CC and the capacity to transfer memory traces between hemispheres would need to be confirmed by neuroimaging studies, using, for instance, diffusion tensor imaging (Beaulieu, 2002). Additionally, investigating gender and handedness as variables would be necessary, given known differences in brain organization among individuals. Indeed, a stronger brain asymmetry is commonly found in male and right-handed individuals, relative to female and left-handed individuals, respectively, across a range of visual, auditory, and tactile laterality tasks (see the review by Himstein et al., 2019).

The current investigation also ought to inspire subsequent research endeavors aimed at examining the relationship between the reduced interhemispheric transfer of simple visual memory traces associated with ageing and the overall age-related decline evident in VWM (Brockmole et al., 2008; Brockmole & Logie, 2013; Brown & Brockmole, 2010; Bruyer & Scailquin, 1999; Chen & Naveh-Benjamin, 2012; Ko et al., 2014; Nicholls & English, 2020; Noack et al., 2012; Peich et al., 2013; Pertzov et al., 2015; Peterson & Naveh-Benjamin, 2016; Rhodes et al., 2017; Tas et al., 2020). The underlying mechanisms for age-related decline in VWM are likely to be multifarious and may include lower perceptual abilities (Faubert & Bellefeuille, 2002; Sara & Faubert, 2000; Schneider & Pichora-Fuller, 2000; Tagliabue et al., 2020), slower processing speed (Gazzaley et al., 2008; Zanto et al., 2010), reduced efficiency of executive attentional capacity (Braver & West, 2011; Gazzaley et al., 2005, 2008; Jost et al., 2011; Reuter-Lorenz & Lustig, 2016; West, 1999), and decreased ability to maintain the stored visual information (Beigneux et al., 2007; Leonards et al., 2002; Palladino & De Beni, 1999). Proposed alterations associated with ageing, encompassing

changes at the neural level such as diminished occipital (Davis et al., 2008; Grady, 1996; Payer et al., 2006; Spreng et al., 2010) and frontal (Milham et al., 2002; Reuter-Lorenz, 2002) cortex activation during perception, attention, and working memory tasks, have been suggested to contribute to the decline in VWM. The present study implies that older adults might exhibit a reduced ability to transfer VWM traces between hemispheres, which could potentially be an additional factor to the overall age-related decline in VWM.

In conclusion, the present findings contribute to the growing body of evidence linking age-related CC degeneration to cognitive decline. The observed decline in VWM performance among older adults, particularly when interhemispheric communication is required, emphasizes the functional relevance of CC integrity for higher cognitive processes. The findings of the present study provide a solid basis for future research into the underlying neural mechanisms underpinning the observed age-related differences. Furthermore, the one-back task employed in this study has theoretically the potential to be used and manipulated to investigate certain clinical conditions characterized by reported abnormalities of the CC, such as Alzheimer's disease and mild cognitive impairment (Di Paola et al., 2010).

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