The relationship between short- and long-term memory is preserved across the age range

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Abstract

The aim of the current study was to examine cross-sectionally the changes in the relationship between short- and long-term memory with age. In two experiments, participants across the age-range were tested on contextual-spatial memories, after short and long memory durations. Experimental control in stimulus materials and task demands enabled analogous encoding and probing for both memory durations. Across the two experiments, we found both short-term memory and long-term memory declined from early to late adulthood in healthy participants. Additionally, there was a significant relationship between short- and long-term memory performance which persisted throughout the age-range. Our findings suggest a significant degree of shared vulnerability for short- and long-term memories sharing the same spatial-contextual associations. Furthermore, our tasks provide a sensitive and promising framework for assessing and comparing memory function at different timescales in disorders with memory deficits at their core.

Introduction

Memories at short and long timescales are highly interconnected. Information extracted from the environment and held over the short term ultimately forms our long-term memories (Atkinson & Shiffrin, 1968; Shiffrin & Atkinson, 1969); in turn, our past experiences bias our short-term memories (Baddeley, 2000; Hebb, 1961; Oberauer et al., 2018). However, few studies have specifically explored the co-variations between short-term memory (STM) and long-term memory (LTM) for the same material (Baddeley, 2012; Brady et al., 2013; Brown et al., 2007; Cowan, 1995; Forsberg et al., 2020; Fukuda & Vogel, 2019; Khader et al., 2007; Oberauer, 2002; Ranganath et al., 2005; Schurgin et al., 2020). In the case of spatial-contextual associations, for example, both memory functions decline with advancing age (Gorbach et al., 2017; Henson et al., 2016; Nilsson et al., 1997; Peich et al., 2013; Pertzov et al., 2015; Rönnlund et al., 2005; Zokaei et al., 2020), and a greater degree of memory preservation in both cases indicates healthy ageing (Pudas et al., 2013; Rogalski et al., 2013; F. W. Sun et al., 2016). This broad pattern therefore suggests a shared vulnerability of short- and long-term memories to age-related processes.

Spatial-contextual short- and long-term memories may share some underlying neural mechanisms, which can result in the observed vulnerability of both memory functions to ageing. For example, the essential role of the medial temporal lobe (MTL) in episodic LTM has been evident at least since the early lesion studies, which showed that individuals with damage to this part of the brain, including the hippocampus, could not form new long-term memories that can be consciously accessed (Milner et al., 1968; Scoville & Milner, 1957; Squire, 2009). Recent studies have shown that the MTL is also crucial for retaining features bound, specifically object-location associations, together in STM (Olson, Page, et al., 2006; Pertzov et al., 2013; Watson et al., 2013; Zokaei, Nour, et al., 2019). Deficits are prominent either when two or more items have to be remembered or when maintaining the exact bindings between objects and their location is necessary for successful performance (Olson, Page, et al., 2006; Pertzov et al., 2013; Watson et al., 2013; Zokaei, Nour, et al., 2019). As a result, it has been proposed that the MTL is involved in the relational binding of representations, irrespective of the memory duration (e.g., Olson, Moore, et al., 2006; Watson et al., 2013, although see Baddeley et al., 2011; Jeneson & Squire, 2012).

To test whether aging-related changes influence a shared set of processes critical to both memory durations, it is useful to test whether the pattern of co-variation remains consistent over a broad age range. Although similar patterns of deficits have been noted, studies to date have not compared performance for STM and LTM directly at multiple ages while also controlling for extraneous factors that could affect performance. To chart the relation between STM and LTM, it is essential to vary only the lifetime of the memory, while keeping the contents of the memoranda and task demands the same. Due to the use of different stimulus materials, task requirements, and output measures across studies, the extent of the overlap between STM and LTM and how they covary in healthy ageing remain unclear.

Studies that have attempted to probe memories derived from common encoding tasks are few and often test short- and long-term memories using different methodologies (e.g., Lugtmeijer et al., 2019; van Geldorp et al., 2015). For example, in one study, performance on a delayed match-to-sample STM task in young, middle-aged, and older adults was compared to two-alternative forced-choice surprise LTM recognition (van Geldorp et al., 2015). Alternatively, another study that assessed young and older adults, contrasted memory for item identity in a two-back STM task with LTM recognition of incidentally encoded object-quadrant associations (Lugtmeijer et al., 2019). Not surprisingly, results across studies have led to a mixed picture of the co-variation between STM and LTM among age groups, with one study

finding no differences (van Geldorp et al., 2015) and the other finding a reduced correlation between STM and LTM in older adults (Lugtmeijer et al., 2019).

Other studies have utilised similar but not identical tasks to encode analogous STM and LTM associations. For example, a study, conducted by Korkki et al. (2020) tested associative memories for object-colour bindings at both short and longer durations. Participants performed two separate continuous-report tasks. In the STM task, they were first shown a display with three coloured objects followed by a memory delay of one second. Following the delay, participants had to adjust the colour of one of the objects, probed by location, to match that of the original object in the memory array. In contrast, in the LTM task, participants viewed five displays of three coloured objects one at a time separated by an interval of one second. The colour-report task then followed a 30-second delay. Participants had to recall and adjust the colours of all 15 objects they had observed in the preceding displays. They found that LTM precision declined disproportionately with age as compared to STM precision (Korkki et al., 2020). Although these tasks probed analogous associations in both timescales, and their continuous-report nature add significant sensitivity and granularity to the measurements, the relationship between these two memory functions may have been understated. Despite similarities between the two tasks, important details may have caused differences in encoding strategy and response variability. STM was probed for one item out of three held in memory, while all fifteen items retained in long-term memory were probed sequentially. This sequential retrieval of object-colour associations could further have added more variability to the LTM as compared to the STM performance, possibly due to a greater interference from previously recalled stimuli (Kiyonaga et al., 2017; Makovski & Jiang, 2008; S. Z. Sun et al., 2017)

The aim of the current study was to explore the changes in the relationship between short- and long-term memories across the age range with a high level of experimental control and equivalent tasks distinguished only by the duration of memory tested. We set out to investigate this relationship using tasks that utilise equivalent stimulus materials and response demands. We used a common encoding phase to assess memory at both short and long durations, for the same type of contextual-spatial associations in young, middle-aged, and older adults cross-sectionally. Short- and long-term memories for this type of information are thought to be dependent on the MTL (Bohbot et al., 1998; Pertzov et al., 2013; Stepankova et al., 2004; Zokaei, Nour, et al., 2019) and particularly vulnerable to ageing (Gorbach et al., 2017; Henson et al., 2016). Here we asked whether aging-related decline in these spatial-contextual associations occurred in the same way and to a similar extent within the different age groups. A shared, age-sensitive mechanism for memory decline across memory time scales would be supported by an overall decline for both STM and LTM across the age groups combined with similar patterns of performance deficits and a strong relationship between STM and LTM performance within each age group.

Experiment 1

Methods

Participants

The study was approved by the Medical Sciences Interdivisional Research Ethics Committee of the University of Oxford in accordance with the Declaration of Helsinki. In total, 65 healthy volunteers took part in this study. Five participants were excluded from the analysis: two due to poor performance (see the Data Analysis section below), one due to an experimenter error, and two due to Addenbrooke's Cognitive Examination 3rd edition (ACE-III) scores < 88, which is the highest recommended cut-off to detect cognitive impairment (Hsieh et al., 2013). This left a sample of 20 young (19-39 years), 20 middle-aged (41-58), and 20 older adults (62-79 years) (see Table 1 for demographics). The sample size was based on a power analysis of predicted effect sizes from a small pilot study.

Participants were members of the local community recruited via Friends of OxDARE participant registry (https://oxfordhealthbrc.nihr.ac.uk/our-work/oxdare/public/become-a-friend/), the Oxford Psychology Research participant recruitment scheme, online advertisement, or word of mouth. All gave written informed consent. They either received course credit or were reimbursed at a rate of £10 per hour for participation. All participants had normal or corrected-to-normal visual acuity and normal colour vision by self-report. The three groups were comparable on years of education. Middle-aged and older adults were comparable on their ACE-III scores (**Table 1**).

Table 1. Descriptive information. ACE-III = Addenbrooke's Cognitive Examination III. Age, years in education and ACE-III scores are presented as mean (SD).

	Young	Middle-aged	Older	p
n	20	20	20	-
Age	25.2(4.9)	49.6 (7.0)	70.8 (4.4)	-
Male/Female	11/9	6/14	9/11	.28
Years in education	17.8 (2.4)	17.5 (3.4)	16.8 (4.6)	.66
ACE-III Total	-	96.5 (2.8)	96.2 (2.1)	.67

Stimuli

Stimuli were presented on a Dell OptiPlex 9030 All-in-One touch screen computer with a 1920-by-1080 pixel resolution (53.0 by 29.7 cm), using the Cogent 2000 toolbox and Matlab release 2015b.

Coloured photographs of complex indoor and outdoor scenes and images of everyday objects were used as stimuli. The scene set consisted of a combination of royalty-free images and photographs from an in-house repository. Ninety-six scenes were randomly selected from a pool of 192 scenes for each participant. They were presented at a resolution of 1125 by 884 pixels (31 by 23.2 cm) surrounded by a grey background (RGB: [0.5, 0.5, 0.5]).

A total of 268 objects were randomly drawn from a pool of 422 coloured objects for each participant. The pool was derived from a combination of experimental stimulus sets available

online (Brady et al., 2008; Brodeur et al., 2010) and copyright-free object images available through Google Images, processed to remove backgrounds when necessary. They included a range of household, food, clothing items, toys, and sports equipment. All objects were sized to fit within a region of 75-by-75 pixels.

Objects were placed randomly within scenes with several restrictions. They were at least 50 pixels away from the edges and from the centre of the screen. In three-object trials, a minimum of 500 pixels separated the centre of the objects. Objects had equal probability of appearing in the four quadrants of the scene.

Tasks and procedures

The study consisted of two stages, in which participants reported the identity and location of objects associated with scenes based on their short-term or long-term memories for those associations, respectively.

In the first stage, participants explored scenes with one or three embedded objects for 5 seconds. In half of the trials, they were probed about the identity of an object in the scene and reproduced its location after a blank interval (8 sec) (STM trials – Figure 1a). In the remaining half of the trials, they explored the scene in a similar fashion, but were not probed for object identity and location following a blank delay (8 sec) (Encoding trials – Figure 1a). These trials were employed to assess LTM for the same type of information encoded in the same way in the subsequent stage of the study.

The second stage was a surprise LTM retrieval performed after a break of approximately 20 minutes (LTM retrieval – Figure 1b). Participants viewed previously learned scenes and were probed about the identity of an object previously presented in the scene. They reproduced its location in a similar fashion to STM trials of the first task, but this time based on their long-term memories.

During the break, young participants completed an online questionnaire on demographic details and their general physical and mental health. During the equivalent period, middle-aged and older participants completed the ACE-III, which was used to screen participants for any signs of cognitive impairment. These two groups completed the online questionnaires at the end of the testing session.

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Figure 1

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Encoding and short-term memory task

A schematic of the combined Encoding and STM trials is shown in Figure 1a. Participants were first presented with a memory array in which either one or three objects were placed within a scene. The array appeared for 5 seconds. Participants first had to find the embedded object(s) and remember their identity(ies) and location(s). The memory array was followed by a delay of 8 seconds, during which participants were presented with a blank grey screen (RGB: [0.5, 0.5, 0.5]).

In half of the trials, the memory delay was followed by STM retrieval (STM trials). The scene from the memory array reappeared with two objects below. One of these objects had previously been embedded in the scene (target), while the other was a completely novel object from any

category (foil). Participants had to identify the target object by tapping on it (identification) and then place the object as precisely as they could in its original location within the scene (localisation) using their finger by either dragging the object or tapping on the screen in the remembered location. Participants were encouraged to respond as quickly as they could when choosing the target object and to prioritise precision when reproducing its location. Once they were satisfied, they pressed the spacebar to proceed to the next trial.

The other half of trials included only the encoding of the object(s) in the scene (Encoding trials). The memory delay was followed by the presentation of the scene with a green fixation cross at the centre. In these trials, participants tapped the fixation cross and pressed the spacebar to continue to the next trial. Participants would subsequently be probed about the object-scene associations in the later, surprise long-term memory task, though they were not informed about this at this stage.

This task consisted of two blocks of 48 trials each. One third of trials contained one object, while the remaining two thirds contained three objects. The two trial types were randomly intermixed across the two blocks, as well as STM and Encoding trials. Therefore, at the time of encoding the identity and location of object(s) in the scene, participants did not know when their memory would be tested, ensuring that encoding strategy as well as any state variables within the experimental block were equated.

All participants completed a minimum set of eight practice trials in order to become familiar with the procedures before the main experimental task. A separate set of scenes and objects was used for these trials. If required, participants could repeat the set of practice trials until they were comfortable with the task.

Explicit long-term memory retrieval

Participants completed a surprise LTM task after a 20-minute break (Figure 1b – LTM retrieval task). In each trial, the procedure for LTM retrieval was equivalent to that used earlier for STM trials. A previously studied scene from the Encoding trials appeared with two objects underneath. One of the objects had been previously embedded in the scene (target), while the other one was a completely novel object from any category (foil). Participants first had to choose the target object (identification) and then drag it to its remembered location (localisation). Once they were satisfied with their response, they pressed the space bar. Following identification and localisation of the remembered item, participants then completed two consecutive confidence rating scales, one for identification and one for localisation, respectively. They reported confidence in their performance on a continuous scale from “Not confident at all” (left) to “Very confident” (right) by moving a scale bar on the screen (results are not reported in the current paper).

This task consisted of one block of 48 trials, which probed memories of only the Encoding trials from the previous stage.

Data Analysis

Data were pre-processed and analysed using MATLAB Release 2018b and R version 4.0.2 (2020) on R Studio version 1.3.1093. Trials were excluded from the analysis if identification times were faster than 100 ms or if localisation occurred outside the scene boundaries. In total, approximately 1% of trials were excluded. Additionally, only the trials in which targets were accurately identified were included in the analysis of identification time and localisation error. Finally, participants were only included in the analysis if their STM localisation performance

was within three standard deviations from the group mean. As a result, two young participants were excluded from all analyses due to poor performance in the one-object STM trials.

Data were not normally distributed. Due to the differences in skewness between STM and LTM, there were no appropriate transformations that would allow us to include data across both durations in the same parametric analyses. Therefore, non-parametric rank-based mixed factorial models were used to analyse identification accuracy, response time, and localisation error data. They were implemented using *nparLD* package version 2.1 on R. The age factor (young, middle-aged, and older groups) varied between participants. Memory duration (STM, LTM) and set size (1 and 3 objects) were manipulated within participants. ANOVA-type statistics (*ATS*) are reported due to their suitability for smaller samples, and modified *ATSs* (ATS_{Mod}) with Box approximation were used for the between-subject factor of age-group (Brunner & Puri, 2013; Noguchi et al., 2012). Where multiple comparisons were made between the three age groups, Mann-Whitney U tests were used, and *alpha* level was Bonferroni-adjusted for the three comparisons.

Chance-level performance for localisation error was estimated by randomly shuffling each participant's response coordinates across all trials and calculating a new localisation error from the original target location to the shuffled response location for every trial. This procedure was repeated for 1000 iterations per participant and per memory type (STM, LTM). Mean localisation error was calculated across all iterations for each participant, and the mean across participants for each memory type and the overall mean across memory types for chance level localisation error.

To explore the relationship between STM and LTM identification times and localisation errors across age groups, general linear models (GLMs) were fitted to mean LTM identification time and localisation error data per participant. Only data from 3-object trials were used. These trials comprised two-thirds of the overall trial number, making the resulting data more robust to noise. The initial models included mean STM identification time per participant and age group as predictor variables for LTM identification time. Mean STM localisation error per participant and age group were used as predictor variables for LTM localisation error. Both models also included an interaction term between the two predictor variables (STM identification time x Age group and STM localisation error x Age group, respectively). Based on the results, two additional simplified models were also fitted for each initial model: one excluding the interaction term and one excluding both the age group and the interaction term, with only the STM measures as predictors.

Results

Identification Performance

There was a significant main effect of age group on identification accuracy ($ATS_{Mod}(1.83, 48.29) = 8.98$, $p = .001$). Follow-up Mann-Whitney U tests showed that, under *alpha* = .017, older adults were significantly less accurate than both young ($U = 7500.5$, $z = 3.69$, $p < .001$) and middle-aged adults ($U = 7208.5$, $z = 2.66$, $p = .008$) (Figure 2a – Identification, upper panel). However, there was no difference in accuracy between young and middle-aged adults ($U = 6711$, $z = 0.96$, $p = .34$).

There were also significant main effects of memory duration ($ATS(1, \infty) = 240.25$, $p < .001$) and set size ($ATS(1, \infty) = 16.63$, $p < .001$), accompanied by a significant interaction between the two factors ($ATS(1, \infty) = 5.96$, $p = .01$). Overall, participants were less accurate when identifying objects from LTM compared to STM and in three-item trials compared to one-item

trials (Figure 1b). Moreover, an interaction revealed the difference in accuracy between one- and three-object trials was only statistically significant in STM ($ATS(1, \infty) = 33.76$, $p < .001$), but not in LTM ($ATS(1, \infty) = .01$, $p = .91$). None of the other interactions reached statistical significance (see Supplementary Table 1S).

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Figure 2

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A similar pattern of findings was obtained for response times in the identification report. There was a significant main effect of age group on identification time ($ATS_{Mod}(1.95, 54.24) = 11.00$, $p < .001$). Follow-up Mann-Whitney U tests showed that, under *alpha* = .017, older adults were significantly slower when identifying targets than both young ($U = 5265.00$, $z = -4.01$, $p < .001$) and middle-aged adults ($U = 5576.00$, $z = -2.95$, $p = .003$) (Figure 1a – lower panel). In contrast, there was no difference in identification times between young and middle-aged adults ($U = 6201.00$, $z = -0.82$, $p = .42$).

There were also significant main effects of memory duration ($ATS(1, \infty) = 524.26$, $p < .001$) and set size ($ATS(1, \infty) = 102.95$, $p < .001$), accompanied by a significant interaction between the two factors ($ATS(1, \infty) = 50.64$, $p < .001$). Overall, participants were slower when identifying objects from LTM compared to STM and in three-item trials compared to one-item trials (Figure 1b – lower panel). Moreover, the interaction revealed the difference in identification time between one- and three-object trials was only statistically significant in STM ($ATS(1, \infty) = 141.64$, $p < .001$) but not in LTM trials ($ATS(1, \infty) = 1.70$, $p = .19$). None of the other interactions reached statistical significance (see Supplementary Table 1S).

Localisation Error

There was a significant main effect of age group on localisation error ($ATS_{Mod}(1.89, 51.03) = 21.61$, $p < .001$). Follow-up Mann-Whitney U tests showed that, under *alpha* = .017, and similar to identification accuracy, older adults produced significantly larger localisation errors than both young ($U = 5434$, $z = -3.43$, $p < .001$) and middle-aged adults ($U = 5557$, $z = -3.01$, $p = .003$) (Figure 1b). There was no difference in the magnitude of localisation error between young and middle-aged adults ($U = 6303$, $z = -047$, $p = .64$) (Figure 2a - Localisation).

There were also significant main effects of memory duration ($ATS(1, \infty) = 1080.58$, $p < .001$) and set size ($ATS(1, \infty) = 141.98$, $p < .001$). Moreover, the two factors of memory duration and set size interacted ($ATS(1, \infty) = 5.85$, $p = .02$). This interaction showed that although overall memory errors were larger in LTM and for larger set sizes, the difference between set sizes was proportionally greater in STM ($ATS(1, \infty) = 209.26$, $p < .001$) compared to LTM ($ATS(1, \infty) = 40.40$, $p < .001$). There were no other significant interactions.

Relationship between short- and long-term memories

To explore the relationship in performance between the two memory durations, we first ran a GLM that included STM identification response time and age group as predictors, and a two-way interaction term between these two factors. The model showed that STM identification response times significantly predicted LTM identification response times ($F(1,54) = 17.26$, $p < .001$). Namely, participants who were slower when identifying targets from STM were also more likely to be slower for LTM, with higher identification response times (Figure 3a). On

the other hand, after accounting for the variation in STM identification response times, the main effect of group and the interaction were not statistically significant (*ps* > .09). This indicated that STM identification response times and not participants' age group best accounted for their response times when identifying targets from LTM, and that participants' age did not alter the relationship between STM and LTM identification response times.

Next, we simplified this model by first removing the interaction term and then the age group. This did not significantly impair model fits (p= .09 and p= .34 respectively); further demonstrating that STM identification response times alone significantly predicted LTM response times ($F(1, 58) = 64.46$, $p < .001$, $R^2 = .53$).

We then ran another GLM to explore the relationship between STM and LTM localisation errors in a similar way. The initial model included STM localisation error and age group as predictors, and a two-way interaction term. The model showed that STM localisation errors significantly predicted LTM localisation errors ($F(1, 54) = 10.2$, $p = .002$). Namely, participants who produced larger STM error were also more likely to produce larger LTM localisation error (Figure 3b). The main effect of age group and the interaction between age group and STM error were not statistically significant (*ps* > .8). This indicated that the magnitude of STM localisation error and not participants' age group best accounted for the magnitude of LTM localisation error, and that age of participants did not mediate the relationship between STM and LTM error.

Next, we simplified this model by first removing the interaction term and then the age group. This did not significantly impair model fits ($p = .8$ and $p = .95$ respectively); further demonstrating that STM errors alone significantly predicted LTM errors ($F(1, 58) = 17.23$, $p < .001$, $R^2 = .23$).

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Figure 3

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In summary, both short- and long-term memories were impaired in older adults. Further, there was a relationship between memory at these two durations which was not altered by participants' age.

In Experiment 2, we sought to replicate our results and go one step further in an on-line study by equating encoding of the short- and long-term memory trials while avoiding close-to-floor performance observed in Experiment 1 in the LTM task, especially in older adults. To this end, in Experiment 2, participants were informed about the time in which they would be probed on object-location associations just after encoding. More specifically, after the encoding of the memory array, a duration cue was presented. In STM trials, the "For Now" duration cue indicated that participants would be probed on their memory in that same trial. In the encoding trials, the "For Later" duration cue indicated that the participant would have to recall the information later, during the LTM retrieval stage of the experiment. Importantly, the timing of the duration cue ensured a common encoding phase for both memory durations. Lastly, to maximise the number of trials for analysis, and further avoid close-to-floor performance in LTM task, we reduced the number items to two per scene. In the interest of time, we also opted to reduce the length of the STM maintenance period to five seconds.

Experiment 2

Participants

The study was approved by the Medical Sciences Interdivisional Research Ethics Committee of the University of Oxford and complied with the Declaration of Helsinki. In total, 70 volunteers, across the age range, took part in this study (the sample size was estimated based on pilot data). Participants were recruited via the Prolific Platform. They gave informed consent and were reimbursed at a rate of £7.5 per hour for participation. All participants had normal or corrected-to-normal vision and normal colour vision by self-report. One participant reported a Parkinson's disease diagnosis and was excluded from the analysis. The final cohort included 69 participants (43 female), between 20 to 79 years of age and with an average of 17.4 (SD: 3.3) years in full-time education.

Stimuli

Coloured photographs of complex indoor and outdoor scenes and images of everyday objects were used as stimuli. The scene set consisted of a combination of royalty-free images and photographs from an in-house repository. Forty-four scenes (similar to Experiment 1) were randomly selected from a pool 399 scenes for each participant in addition to 132 objects that were randomly drawn from a pool of 135 coloured objects. The objects (0.5 visual degrees) were selected from emoticons of everyday objects (https://emojipedia.org/) and included a range of household, food, clothing items, toys, and sports equipment.

At the start of the experimental session, participants' screen resolution was estimated by asking them to adjust an image of a credit card to match the size of a physical credit card. We therefore could calculate the ratio between the card image width in pixels and the actual card width in centimetres. This allowed us to obtain a measure of pixel density (i.e., pixel per cm). In turn, this allowed us to control the size of the stimuli in degrees of visual angle in approximate terms by instructing participants to the view the monitor at one arm's length distance (approximately 60 cm) (Li et al., 2020).

Objects were placed randomly within scenes with several restrictions. They were at least 1.5 visual degrees away from the edges and from the centre of the screen. There was a minimum of 2.5 visual degrees between the centre of the objects in the two-object trials. Objects had equal probability of appearing in the four quadrants of the scene.

Tasks and procedures

Similar to Experiment 1, this study consisted of two stages, in which participants reported the identity and location of objects associated with scenes based on their short-term or long-term memories for those associations, respectively (Figure 4).

In the first stage, participants explored scenes with two embedded objects for 5 seconds. After a 1-second delay, they were presented with a duration cue, indicating the time in which they would be probed. In half of the trials, following the "For Now" cue (0.5 sec) and a blank interval (3.5 sec), participants were probed about the identity of an object in the scene and reproduced its location (Figure 4a – STM trials). In the remaining half of the trials, following the "For Later" cue (0.5 sec) and a blank interval (3.5 sec), participants were presented with the scene without the objects embedded within them and had to press the fixation as soon as it turned green. These trials were employed to assess LTM for the same type of information later in the study (Figure 4a – Encoding trials).

The second stage involved an LTM-retrieval task (Figure 4b – LTM retrieval) performed after a break of approximately 15 minutes. Participants viewed previously learned scenes and were probed about the identity of an object previously presented in the scene and reproduced its location in a similar fashion as in the first task (STM trials), but this time based on their long-term memories.

During the break, participants completed an unrelated task online that took around 10 minutes. They were encouraged to take breaks before and after this task. Importantly, the intervening task did not involve any objects or scenes.

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Figure 4

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Short-term memory/Encoding task

In this stage of the experiment (Figure 4a), participants were first presented with a memory array in which two objects were placed within a scene. The array appeared for 5 seconds. Like Experiment 1, participants first had to find the embedded objects and remember their identities and locations. The memory array was followed by a delay of 1 seconds, during which participants were presented with a blank grey screen. This was then followed by a duration cue ("For Now" or "For Later" at centre of the screen), presented for 0.5 seconds, indicating the duration in which participants had to keep the information in mind.

In trials containing the "For Now" cue (Figure 4a - STM trials), participants were probed after a 3.5 second blank delay. At retrieval, the scene from the memory array reappeared with two objects below. One of these objects had previously been embedded in the scene (target), while the other was an object not seen in the scene (foil). Participants had to identify the target object by pressing the letter C to choose the object on the left or the letter M to choose the object on the right. They then had to use the mouse cursor to click the original location of the object within the scene (localisation). Participants were encouraged to respond as quickly as they could when choosing the target object and to prioritise precision when reproducing its location. Once they were satisfied, they pressed the mouse button to proceed to the next trial.

In the other half of trials, the "For Later" cue was followed by a delay (3.5 sec) and the presentation of the scene (Figure 4a - Encoding trials). Participants had to click the fixation cross as soon as it turned green (after 1 second) to continue to the next trial. Participants would subsequently be probed about the object-scene associations in the later long-term memory task.

The task consisted of two blocks of 20 trials each. The two trial types (For Now and For Later) were randomly intermixed across the two blocks. All participants completed four practice trials prior to the task to become familiar with the procedures. A separate set of scenes and objects was used for these trials.

Explicit long-term memory retrieval

Participants completed an LTM task after a break of approximately 15 minutes (Figure 4b – LTM retrieval). In each trial, the LTM retrieval stage was equivalent to that used earlier for STM retrieval. A previously studied scene from the Encoding trials appeared with two objects underneath. One of the objects had previously been embedded in the scene (target), while the other one had not been in the scene (foil). Participants had to select the target object

(identification) and place it in its remembered location (localisation) using the same procedures as in the STM trials. The task consisted of one block of 20 trials.

Data Analysis

Data were pre-processed and analysed using MATLAB Release 2018b. Exclusion criteria were identical to those specified for Experiment 1. Repeated-measures ANOVAs with duration cue as a within-subject factor and age as a covariate were conducted for identification accuracy, identification response times, and localisation errors. Data that were not normally distributed were transformed allowing us to use parametric statistics.

The same procedure was used to estimate chance-level performance for localisation error as in Experiment 1. To explore the relationship between STM and LTM, GLMs were fitted using mean LTM identification time and localisation error data as explained previously.

Results

Identification Performance

Accuracy on the identification tasks showed that performance decreased with age overall, but that the decline was relatively worse in the LTM compared to the STM task. The ANOVA revealed a significant main effect of age ($F(1,67) = 18.75$, $p < .001$, $\eta^2_p = .22$) and a significant interaction between age and memory duration ($F(1,67) = 4.4$, $p = .04$, $\eta^2_p = .06$) on identification accuracy. Memory duration did not exert a significant main effect ($p = .5$). Within tasks, memory decline was significant for both STM ($F(1,67) = 6.8$ $p = .011$, $\eta^2_p = .09$) and LTM ($F(1,67) = 13.86$ $p < .001$, $\eta^2_p = .17$) (Figure 5a).

For identification response times, there were significant effects of both age ($F(1,67) = 28.77$, $p < .001$, $\eta^2_p = .3$) and memory duration ($F(1,67) = 14.25$, $p < .001$, $\eta^2_p = 0.18$). Responses slowed with ageing and were longer in the LTM task. There was no interaction between age and memory duration ($p = 0.6$) (Figure 5b).

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Figure 5

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Identification accuracy in the STM task was high and its low variability precluded analysis of the relationship between performance for the two memory timescales between age groups. However, it was possible to test for the relationship using response times. We used GLM to examine whether variation in STM identification response times and age predicted LTM response times. A model including age and STM performance was a significant predictor of LTM response times, $F(2, 66) = 19.49$, $p < .001$, $R^2 = .24$. Older individuals and individuals who took longer to identify the target items in the STM task were also slow in the LTM task (Figure 6a).

Localisation Error

Age significantly affected the amount of error in the localisation task ($F(1,67) = 14.6$, $p < .001$, $\eta^2_p = .18$). Localisation error increased with age. There was no main effect of memory duration ($p = .1$) or interaction between age and memory duration ($p = .08$) (Figure 5c).

Like in Experiment 1, to explore whether variation in STM localisation error and age predicted long-term memory performance, we used a GLM. A model including age and STM performance was a significant predictor of LTM localisation performance, $F(2, 66) = 8.23$, $p = .001$ $R_2 = .2$. Both variables contributed significantly to the prediction, $p < .05$. Participants with a larger STM error and of increasing age were more likely to produce a larger LTM localisation error (Figure 6b). Additionally, similar to Experiment 1, STM errors significantly predicted LTM errors ($F(1, 67) = 10.6$, $p = .002$, $R^2 = .137$).

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Figure 6

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Discussion

The current study used novel continuous-report tasks that enabled analogous assessment of both short- and long-term memories cross-sectionally across the adult age range. In our first experiment, the findings suggest that older but not middle age brings impairments in both short- and long-term memories. Additionally, there was a significant relationship between short- and long-term memory performance that remained unaltered by the participants' age. The time it took participants to identify the target objects and the magnitude of their localisation error in STM were strong predictors of equivalent performance measures in LTM. Age did not change this relationship. In a follow-up online experiment, we replicated our main pattern of results in a version of the task that avoided near-floor performance in LTM retrieval and using a distribution of ages rather than categorical age groups. In an attempt to equate encoding even further, in this experiment participants were informed about the memory duration using a cue after items were encoded into memory, and prior to the response. They knew, therefore, that encoded associations would remain relevant even if they were not immediately probed on these. Importantly, in both experiments STM performance independently and significantly contributed to LTM performance.

To our knowledge, this is the first time the relationship between memories at the short and long timescales has been assessed for the same content of spatial-contextual associations encoded the same way and retrieved with equivalent task demands. The strong relationships between performance variables across the memory timescales and their invariance to age are consistent with a considerable overlap in functional mechanisms that are sensitive to age. Our results thereby provide indirect support for proposals that memories for bound representations, such as object-location associations, rely on the MTL, regardless of the memory duration (Kolarik et al., 2018; Yonelinas, 2013; Zokaei, Nour, et al., 2019).

STM localisation errors accounted for a significant proportion of variance in LTM localisation errors in both experiments. This variability may have originated from processing during the encoding stage, which was identical for both STM and Encoding trials. Additionally, there may

be other mechanisms that govern variability in both memory systems. For example, apart from their ability to bind item-location associations (Watson et al., 2013; Zokaei, Nour, et al., 2019) and the granularity with which they can store location information in both STM and LTM (Bosch et al., 2014; Serences, 2016), participants' performance may be limited by their ability to exert selective attention in a goal-directed manner to encode and maintain associations. While the ability to bind associations can be assessed using mixture modelling on the localisation error data (e.g., Grogan et al., 2020), here our main goal was to establish the relationship between STM and LTM in a large number of participants. This resulted in an insufficient number of trials per participant to obtain reliable model estimates. Future studies, by employing mixture modelling, can identify the underlying sources of error contributing to the relationship in memory at these two durations (as in Korkki et al., 2020). In addition, differences in encoding can be explored in future studies by systematically varying the length of the encoding period or measuring variability in the neural signatures during encoding stage using brain measures.

The relationship between STM and LTM measured in in both experiments was similar across the age groups, suggesting that both STM and LTM decline at a similar rate with advancing age. The involvement of the MTL and the hippocampus in STM and LTM binding (Kolarik et al., 2018; Yonelinas, 2013; Zokaei, Nour, et al., 2019), as well as alterations in visual functions with age that may affect the granularity of representations (Chamberlain et al., 2021; Jorge et al., 2020; Pitchaimuthu et al., 2017), may explain why the two types of memory have a shared vulnerability to healthy ageing.

However, the question of whether the relationship between the two memory functions is also preserved in pathological ageing remains open. The rare apolipoprotein E (APOE) e4 allele, when contrasted with the common e3 allele, is the strongest genetic risk factor for late-onset Alzheimer's disease (Farrer, 1997). By using two different continuous report tasks to measure STM and LTM for contextual-spatial associations, one study has shown a potential dissociation between STM and LTM performance in the older APOE e4 carrier group as compared to non-carriers (Zokaei, Čepukaitytė, et al., 2019). While carriers performed better than non-carriers in the STM task after a one-second memory delay, their LTM performance was significantly worse than that of non-carries, suggesting that STM and LTM may be differentially affected by genetic risk of dementia, pointing to differences in the neural mechanisms supporting the two memory systems (Zokaei, Čepukaitytė, et al., 2019). It is important to note however that in this study, STM and LTM were tested using different tasks that were not directly comparable. Similarly, one recent study found that the advantage in STM is exaggerated in APOE e4 carriers as compared to non-carriers even in the presence of Alzheimer's disease pathology (Lu et al., 2021). Similar tasks as used in the current study could therefore be useful for characterising STM and LTM performance in APOE e4 carrier and non-carrier groups.

In addition to exploring the relationship between short- and long-term memories, our tasks allowed us to examine memory performance at different durations, independently. Both the ability to recall identities and locations of objects was diminished in older age, for both memory durations. While in Experiment 1, middle-aged adults were comparable in performance to young adults across the board, Experiment 2 showed a more gradual decline in performance with advancing age of participants. Findings from Experiment 1 are consistent with previous reports of STM and LTM impairments from the age of 60 from relatively small studies that treated age as a categorical variable (Korkki et al., 2020; Lugtmeijer et al., 2019; Pertzov et al., 2015; van Geldorp et al., 2015). In contrast, findings from Experiment 2 are comparable to those from larger cross-sectional studies, which have shown a gradual decline in STM and LTM performance across adulthood (Henson et al., 2016; Zokaei et al., 2020). There may be several reasons behind these differences. Firstly, it may simply be due to the fact that age of

our participant was categorical in Experiment 1 and continuous in Experiment 2. Secondly, the findings of Experiment 1 may suggest a selection bias, as the sample was drawn from the local highly educated Oxford population. Cognitive reserve in such individuals may result in preserved memory performance at middle age (Stern, 2012). If this is the case, the use of online tasks may have the advantage of avoiding the selection bias and recruiting participants from a wider range of demographic backgrounds. Finally, memory decline may indeed accelerate later in life, after the age of 60, becoming substantial enough to be detected consistently with a relatively small cross-sectional sample. Notably, both middle-aged and older adults in Experiment 1 showed comparable performance on the ACE-III, which is a standard neuropsychological test of cognition. This provides evidence for the sensitivity and utility of continuous report tasks used in this study for measuring differences in memory functions across groups of otherwise healthy adults, regardless of the in-person or online format.

Interestingly, the memory load manipulation, included only in Experiment 1, affected not just STM but also LTM localisation performance: participants produced larger localisation errors in three-item trials as compared to one-item trials in both tasks. This is surprising given that, in contrast to STM, LTM is thought to have a near-unlimited capacity (Brady et al., 2008). However, this finding could be explained by a limited encoding window. In the study by Brady et al. (2008), although characteristics of hundreds of different objects were encoded into LTM, a three-second time window was dedicated for the encoding of each object. In contrast, Experiment 1 utilised a constant five-second window in both one- and three-item trials, during which participants searched for items within scenes and encoded their identities and locations. It is therefore possible that the constant encoding window of five seconds in the current study has contributed to a reduced per-item encoding in three-item as compared to one-item trials, resulting in consequences on localisation performance across both STM and LTM. In contrast, there was no difference in identification accuracy between set size conditions in LTM trials. This suggests that long-term memories for object identities were less affected by the limited encoding window than short-term memories. Potentially, other mechanisms, such as familiarity, which does not require detailed representations of stimuli (Schurgin, 2018), may have contributed to object identification performance in LTM trials.

One of the potential limitations of this study was that, apart from controlling for self- reported visual abilities, there were no objective measures of visual functions and processing speed. Older adults have been shown to have difficulty ignoring distracting stimuli (Babu et al., 2014). This, in combination with the slower processing speed (Owsley, 2013) and the limited encoding window, may have disproportionately disadvantaged older adults while they were searching for objects in memory displays, especially in Experiment 1. This could have led to disadvantages in localisation performance across memory conditions, as older adults may have not had as much time as the other two groups to explicitly learn object locations after the objects have been found. Although this did not alter the relationship between STM and LTM across age groups in the two experiments, more objective measures of visual functions and processing speed should be included in future studies investigating the effects of ageing on memory using similar tasks.

Overall, we found that ageing impairs both STM and LTM performance but does not alter the relationship between these two memory functions. By introducing a greater experimental control through utilisation of equivalent stimulus material and response demands, we were able to assess memory performance for different durations, in a comparable way. Importantly, our experimental design ensured equal encoding for memory at both durations since participants became aware of the duration only after items were encoded into memory and either at probe (Experiment 1) or during memory duration (Experiment 2). The task proved to be sensitive to age-related changes in performance for both short- and long-term memories and allowed us to

further examine the relationship between the two processes and any changes to this relationship in healthy aging. Therefore, this task provides an opportunity to examine memory function at different timescales in disorders with memory deficits at their core.

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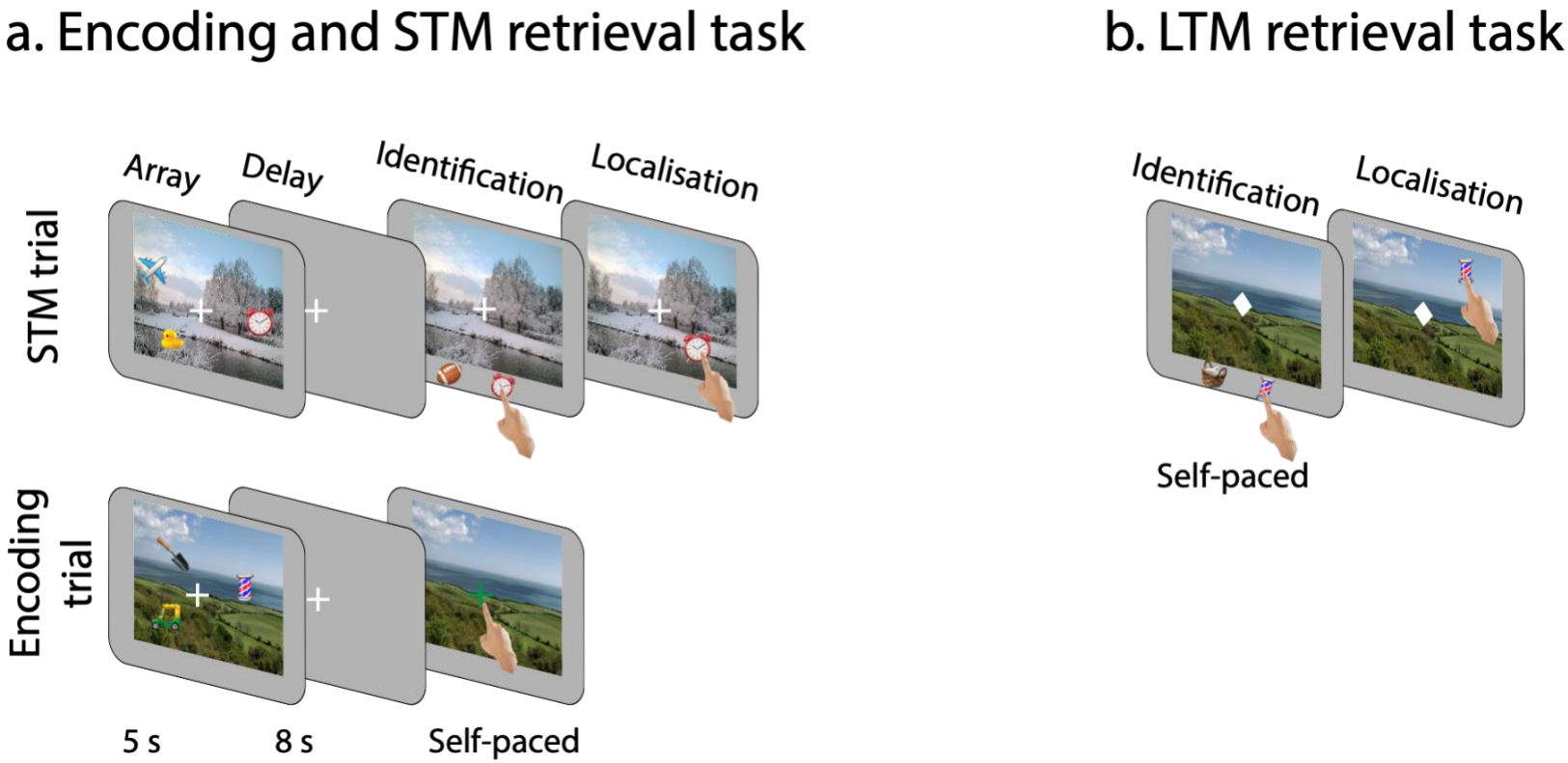

Figure 1. **a. STM/Encoding task in Experiment 1**. Each trial started with a memory array of 1 or 3 objects embedded within a scene, followed by a delay. In the short-term memory (STM) trials, the delay was followed by STM retrieval phase. The memory scene reappeared with two objects underneath. Participants selected the object they had seen in the memory array (identification) and placed it at its original location as precisely as they could (localisation). In the encoding trials, the delay was followed by the scene containing a green fixation marker in the centre of the screen. Participants tapped on the green fixation cross. **b. LTM retrieval task**. Participants completed a surprise LTM task after a 20-minute break. In each trial, the LTM retrieval phase was equivalent to that used earlier for STM retrieval. A previously studied scene appeared with two objects underneath. Participants had to select the object previously presented in the Encoding task and drag it to its location.

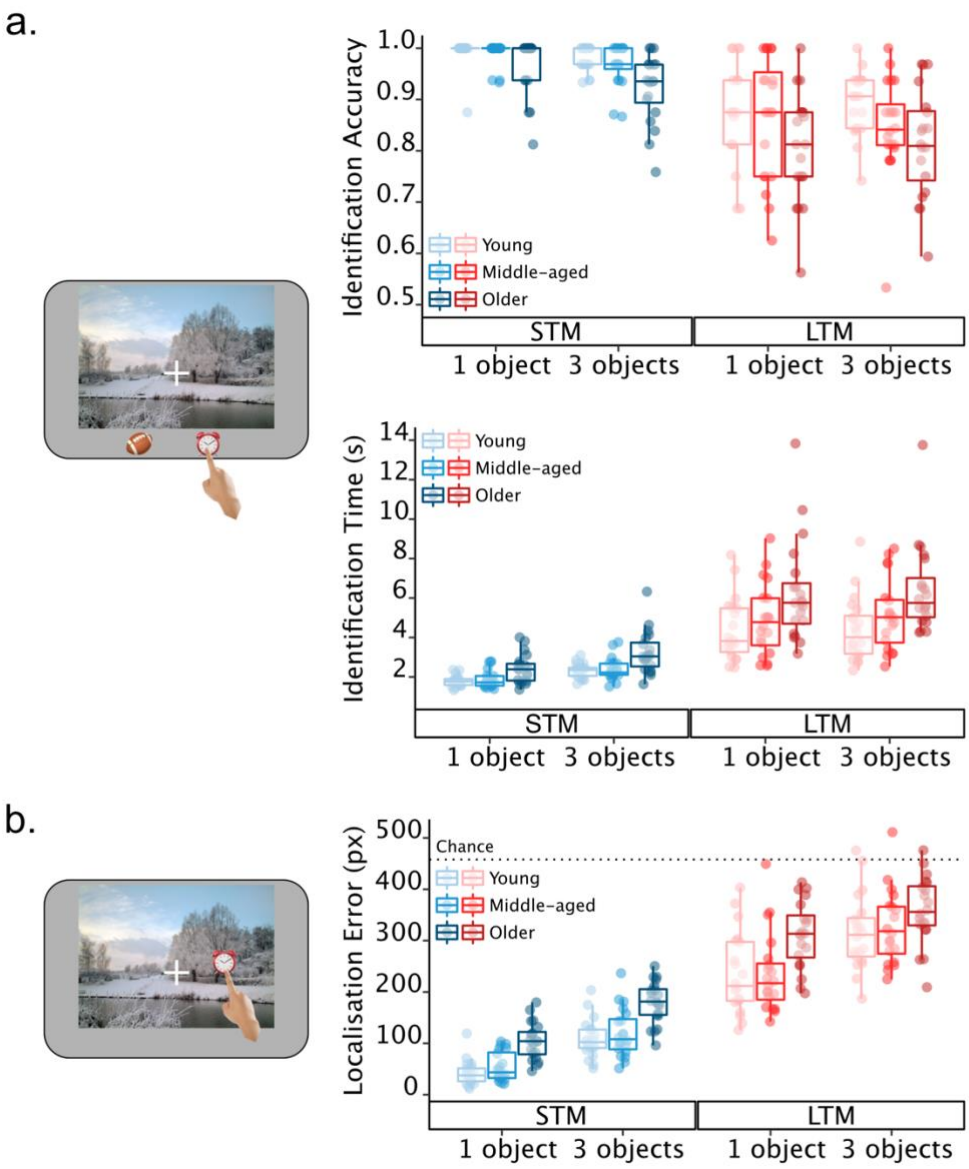

Figure 2. **a. Identification performance and b. Localisation error in Experiment 1.** Overall, older adults performed worse than both young and middle-aged individuals whose performance was comparable across the tasks and for both identification and localisation. Coloured dots represent participant means, lines inside boxes represent group medians, hinges represent first and third quartiles, and whiskers represent values that fall outside the IQR but within 1.5 * IQR from each hinge.

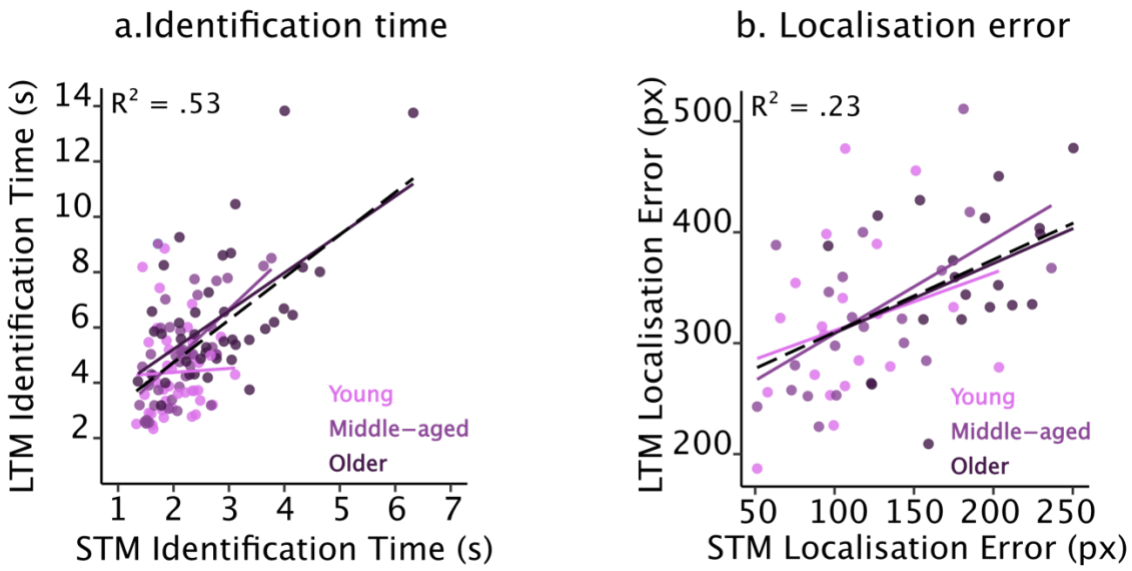

Figure 3. The relationship between STM and LTM for Identification times (a) and localisation errors (b) across age groups for the three object trials in Experiment 1. Coloured dots represent participant means and coloured lines represent regression lines per age group. Dashed black line represents model fit across groups. Regression coefficients are reported for the most parsimonious models only, which was LTM~STM in both cases.

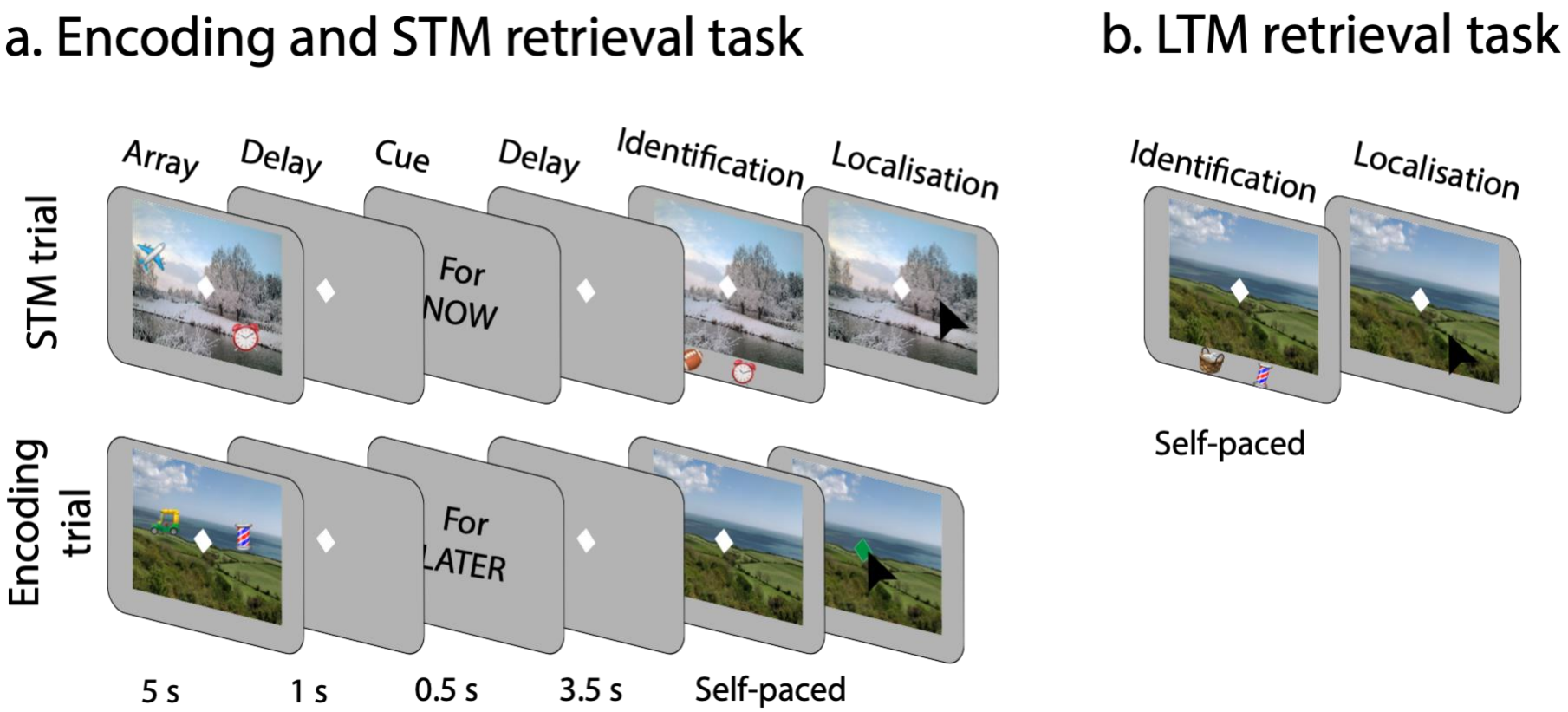

Figure 4. **a. Encoding and STM retrieval task in 3.** Each trial in the encoding and STM task started with a memory array of 2 objects embedded within a scene, followed by a delay before the presentation of the duration cue. This cue was then followed by a blank delay before the presentation of a probe. In the STM trials, the delay was followed by a STM retrieval phase. The memory scene reappeared and, after a delay, two objects appeared underneath. Participants selected the object they had seen in the memory array (identification) and indicated its original location (localisation) as precisely as possible. In the encoding trials, the delay was followed by the scene without the objects and participants had to click the fixation as soon as it turned green. **b. LTM retrieval task**. Participants completed an LTM task after approximately 15 minutes. The LTM retrieval phase was equivalent to that used earlier for the STM retrieval. A previously studied scene appeared and after a delay two objects were presented underneath. Participants had to identify and then localise the object previously associated with the scene in the Encoding task.

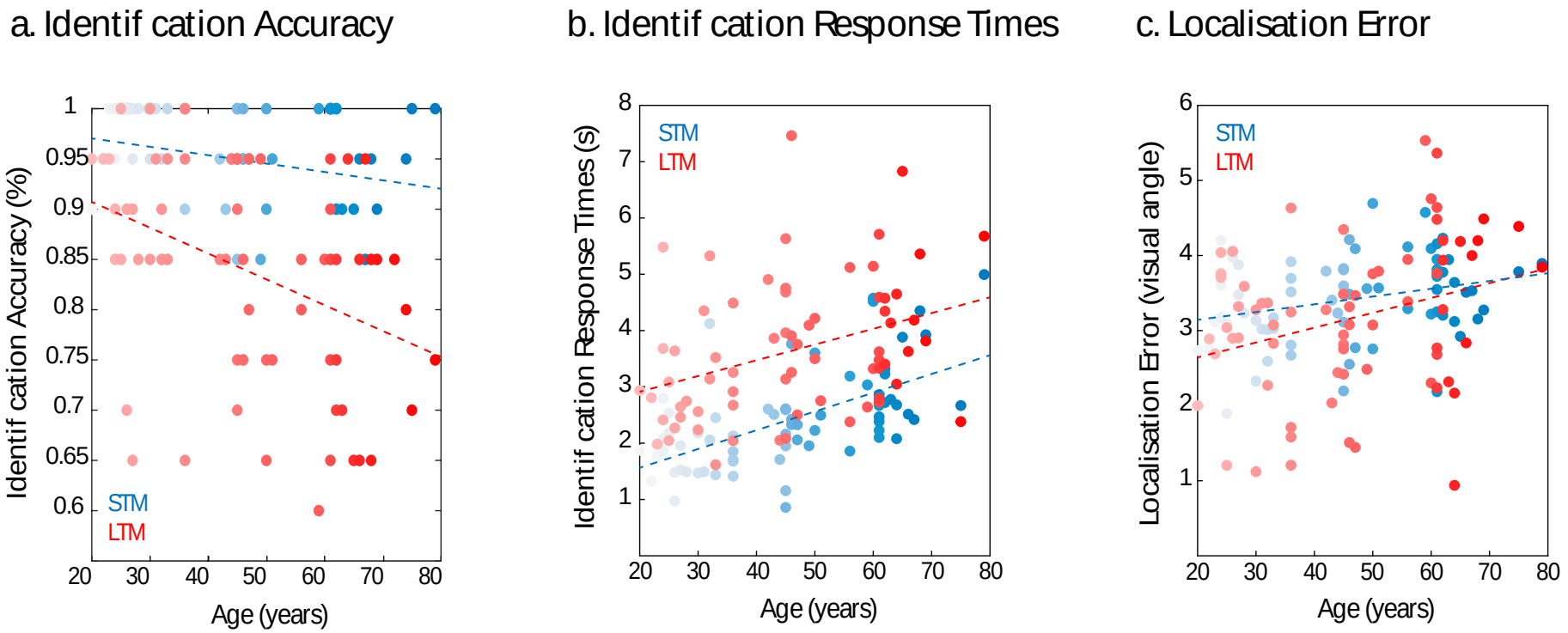

Figure 5. Variation of performance on both STM and LTM retrieval tasks across age in Experiment 2. Dots represent individual participants' means **a. Identification Accuracy**. Overall aging impaired performance on both memory tasks, with worst performance in the LTM trials. **b. Identification Response Times**. Overall, participants were slower in the LTM task and both short- and long-term memory trials were influenced by ageing. **c. Localisation Error**. Performance was significantly less accurate for older than younger adults in identifying the location of the target object. Dots represent individual participants' means.

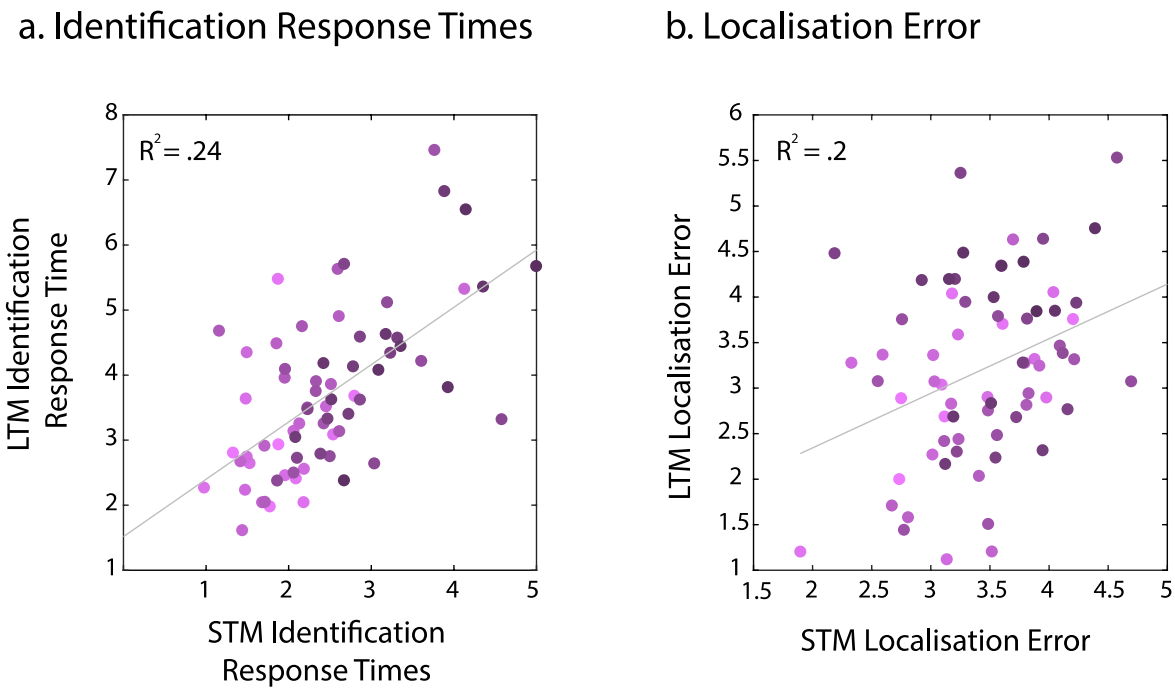

Figure 6. The relationship between STM and LTM for Identification times (a) and localisation errors (b) in Experiment 2. Dots represent individual participants' means. Saturation changes reflect the age of participants.