Healthy Ageing Reduces the Precision of Episodic Memory Retrieval

Saana M. Korkki
University of Cambridge

Franziska R. Richter
Leiden University

Priyanga Jeyarathnarajah and Jon S. Simons
University of Cambridge

Episodic memory declines with older age, but it is unresolved whether this decline reflects reduced probability of successfully retrieving information from memory, or decreased precision of the retrieved information. Here, we used continuous measures of episodic memory retrieval in combination with computational mixture modeling of participants' retrieval errors to distinguish between these two potential accounts of age-related memory deficits. In three experiments, young and older participants encoded stimulus displays consisting of everyday objects varying along different perceptual features (e.g., location, color and orientation) in a circular space. At test, participants recreated the features of studied objects using a continuous response dial. Across all 3 experiments, we observed significant age-related declines in the precision of episodic memory retrieval, whereas significant age differences in retrieval success were limited to the most challenging task condition. Reductions in mnemonic precision were evident across different object features retained in long-term memory and persisted after controlling for age-related decreases in the fidelity of perception and working memory. The findings highlight impoverished precision of memory representations as one factor contributing to age-related episodic memory loss and suggest that the cognitive and neural changes associated with older age may differentially affect distinct aspects of episodic retrieval.

Keywords: aging, episodic memory, long-term memory, working memory, precision

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Episodic memory enables us to recollect details of events from our personal pasts, such as recalling our last birthday party, or where we parked our car on our last visit to the supermarket. Intact memories of our past experiences are vital for developing and maintaining our sense of self (Conway, 2005; Tulving, 2002) and guide the actions and decisions we take in our everyday lives (Schacter, Addis, & Buckner, 2007; Wimmer & Shohamy, 2012), enabling flexible behavior in changing environments. Episodic memory function exhibits marked declines as we grow older (Grady, 2012; Hedden & Gabrieli, 2004), however, with longitudinal studies typically displaying decreases from the age of 60 onward (Nyberg, Lövdén, Riklund, Lindenberger, & Bäckman, 2012; Nyberg & Pudas, 2019). The particular vulnerability of episodic memory to age-related decline in comparison to other cognitive domains, including other types of long-term memory (LTM), has been highlighted in previous studies (Nyberg et al., 2003; Rönnlund, Nyberg, Bäckman, & Nilsson, 2005), but the specific neurocognitive mechanisms underlying this impairment are yet to be fully characterized. In particular, it is unclear whether age-related memory reductions may reflect a decreased probability of successfully retrieving information from memory, or more qualitative changes in the fidelity with which memory traces can be encoded into and retrieved from memory.

In typical laboratory tests of episodic memory, participants' performance is measured using categorical response options, for example by asking a participant to judge whether a test stimulus has been previously encountered ("old") or not ("new"). These types of measures, however, often afford only binary distinctions between successful and unsuccessful memory retrieval, unable to fully capture the multifaceted nature of episodic recollection. In-

creasing evidence suggests that instead of an "all-or-none" process, varying only in the dichotomy between successful and unsuccessful retrieval, episodic recollection likely operates in a "some-or-none" manner, where the quality, or precision, of the successfully retrieved information can vary on a graded scale (Harlow & Donaldson, 2013; Onyper, Zhang, & Howard, 2010; Yonelinas & Parks, 2007). To investigate these more fine-grained variations in episodic memory, recent studies have begun to use continuous measures of retrieval performance, where participants are asked to reconstruct aspects of the studied stimuli using a continuous, analogue scale. In younger adults, studies using these types of tasks have demonstrated retrieval success and precision to be separable components of LTM (Harlow & Donaldson, 2013; Harlow & Yonelinas, 2016; Richter, Cooper, Bays, & Simons, 2016), which can be selectively affected by experimental manipulations (e.g., Sutterer & Awh, 2016; Xie & Zhang, 2017), brain stimulation (Nilakantan, Bridge, Gagnon, VanHaerents, & Voss, 2017), and developmental condition (Cooper et al., 2017). Furthermore, a recent study by Richter et al. (2016) provided evidence for a dissociation between these two mnemonic constructs at the neural level, demonstrating that the success and precision of episodic recollection rely on distinct brain regions of the core episodic memory network, with retrieval success scaling with hippocampal activity and retrieval precision with activity in the angular gyrus. Given the dissociable neurocognitive profiles of these two subcomponents of episodic memory retrieval in younger adults, it is therefore possible that they may also be differentially sensitive to age-related cognitive decline.

Several strands of evidence imply that memory function in older age might at least to some extent be constrained by reductions in the quality and specificity of information retained in memory. For example, age-related increases in false memory have been interpreted as resulting from increased reliance on gist-like representations of previous events with diminished encoding and retrieval of specific stimuli details (Dennis, Kim, & Cabeza, 2007, 2008; Kensinger & Schacter, 1999; Koutstaal & Schacter, 1997). Furthermore, previous research has demonstrated greater age differences in episodic recollection when participants are required to retrieve more detailed information about the study event (Luo & Craik, 2009), and that older adults tend to recall less specific details of events from their personal pasts in comparison to younger adults (Addis, Wong, & Schacter, 2008; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Despite often preserved ability to recognize studied items as previously encountered, and to identify dissimilar novel items as new, older adults are also typically impaired in mnemonic discrimination of studied items from perceptually similar lures (Stark, Yassa, Lacy, & Stark, 2013; Toner, Pirogovsky, Kirwan, & Gilbert, 2009; Yassa et al., 2011), implying a reduced level of detail of the retained memory representations in older age.

In addition to these behavioral findings, age-related reductions in memory fidelity would be predicted by previous accounts proposing increased neural noise (i.e., increased uncertainty of neural signaling) to lead to more variable and less precise perceptual and cognitive representations in older age (e.g., Welford, 1958, 1981). Consistent with these proposals, age-related increases in discriminal dispersion have been previously demonstrated for short-term memory (STM) retrieval (e.g., Allen, Kaufman, Smith, & Propper, 1998; Noack, Lövdén, & Lindenberger, 2012), and modeled by

age-related increases in internal noise (Allen et al., 1998). Later computational models have further proposed age-related changes in neuromodulation to underlie decreased neural signal-to-noise ratio leading to less precise representations (Li, Lindenberger, & Sikström, 2001; Li & Sikström, 2002). In line with these proposals, more recent findings from functional brain imaging have demonstrated age-related decreases in the fidelity of neural representations corresponding to different stimuli or task contexts during both encoding and retrieval of episodic memory (Abdulrahman, Fletcher, Bullmore, & Morcom, 2017; St-Laurent, Abdi, Bondad, & Buchsbaum, 2014; Trelle, Henson, & Simons, 2019; Zheng et al., 2018), potentially constraining the precision with which memory representations can be formed as well as recovered in older age.

Despite proposals of reduced memory quality in ageing, the majority of previous behavioral investigations have tended to rely on categorical measures of memory performance, which are unable to discern whether age-related performance reductions are due to changes in the success or precision of memory retrieval. For instance, a failure to correctly retrieve a specific study detail in a categorical memory task could reflect either a failure to access the information in question, or decreased fidelity of the retrieved information, leading to selection of an incorrect retrieval response. In working memory (WM) research, continuous report tasks, providing a more direct measure of memory fidelity, have been fruitful in elucidating the specific components of STM degradation in older age, revealing age-related decreases in mnemonic precision and increases in binding errors, whereas no age differences in the success of memory retrieval were detected (Peich, Husain, & Bays, 2013). This approach has recently been extended to investigate age-related changes in object-spatial location binding in LTM, suggesting that the precision of LTM retrieval might similarly be sensitive to age-related decline (Nilakantan, Bridge, Van-Haerents, & Voss, 2018).

The aim of the current study was to use a continuous report paradigm, adapted from recent work in younger adults (Richter et al., 2016), to better characterize the nature of age-related changes in episodic memory. Specifically, we aimed to distinguish whether age-related memory decreases reflect reduced probability of successfully retrieving information from memory, and/or decreased precision of the retrieved memory representations. In a series of three experiments, healthy young and older participants encoded visual stimulus displays consisting of everyday objects varying along different perceptual features (e.g., location, color and orientation) in a circular space. At test, participants were asked to recreate the features of studied objects using a continuous response dial, allowing for detailed assessment of retrieval performance. Fitting a computational mixture model (Bays, Catalao, & Husain, 2009; Zhang & Luck, 2008) to participants' retrieval error data allowed us to estimate both the probability of successful retrieval and the precision of the retrieved information from the same data, distinguishing between these two alternative sources of memory errors in older age.

In the first experiment, we examined the effects of healthy ageing on the success and precision of object location retrieval, revealing age-related decreases in memory precision despite intact probability of successful memory retrieval in the older group. In the second experiment, we assessed whether these age-related deficits in memory precision were specific to the retrieval of

spatial locations or evident across different types of information retained in LTM. Participants encoded and retrieved objects varying in three different perceptual features (location, color and orientation) in a circular space. Although age-related deficits in memory precision were consistently observed across the feature conditions, significant age-related reductions in retrieval success were evident in the orientation condition only, which was also the condition exhibiting the lowest retrieval success in the younger adults. In the third experiment, we examined whether the age-related changes in memory precision were specific to LTM, or whether they might to some extent be explained by potential deficits in the fidelity of perception (Monge & Madden, 2016) or WM (Peich et al., 2013; Pertzov, Heider, Liang, & Husain, 2015). Results from this last experiment indicated that although age-related decreases in representational fidelity were evident in all three tasks (perception, WM, and LTM), the age-related reductions in episodic memory precision persisted after controlling for variation in both perceptual and WM precision, suggesting a predominantly LTM basis for this deficit.

General Methods

In each experiment, participants encoded object stimulus displays and later recreated the features (such as location, color, or orientation) of studied objects as precisely as they could using a 360-degree response dial. Both studied feature values and participants' responses mapped onto a circular space, enabling us to distinguish between the probability of successful retrieval (i.e., probability of retrieving some information about the correct target feature value) and the precision of retrieved information (i.e., variability in successful target retrieval) with a mixture modeling approach derived from WM research (Bays et al., 2009; Zhang & Luck, 2008), but more recently also applied to LTM studies (e.g., Brady, Konkle, Gill, Oliva, & Alvarez, 2013; Richter et al., 2016). At the beginning of each experiment, participants completed a demographic questionnaire and the Shipley Institute of Living Vocabulary Scale (SILVS; Zachary & Shipley, 1986) measure of crystallized intelligence. To exclude any older participants displaying signs of cognitive impairment, the older adults additionally completed the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), a standardized 10-min pen-and-paper screening tool for detection of mild cognitive impairment. Before each of the continuous report tasks, participants completed practice trials of the task.

Participants

Participants for all experiments were native English-speakers who reported normal or corrected-to-normal vision, no color blindness, and no current or historical diagnosis of any psychiatric or neurological condition or learning difficulty. Older participants scored in the healthy range (26 or above) on the MoCA (Nasreddine et al., 2005). Participants gave written and informed consent in a manner approved by the Cambridge Psychology Research Ethics Committee and were compensated for their participation at the rate of £7.50 per hour.

Data Analysis Approach

Retrieval error on each trial was calculated as the angular difference between participants' response value and the target feature value (0 ± 180 degrees). To distinguish between different sources of memory errors (i.e., reduced retrieval success vs. reduced memory precision), a probabilistic mixture model was fitted to participants' error data (Bays et al., 2009; Zhang & Luck, 2008; code available at http://www.paulbays.com/code/JV10/index.php; see Figure 1). In this model, two sources of error contribute to participants' performance: variability, that is, noise, in reporting the correct feature value when information about the target has been retrieved, and a proportion of trials where memory retrieval has failed and responses reflect random guessing. These two sources of error are modeled by two components: a von Mises distribution (circular equivalent of a Gaussian distribution) centered at a mean error of zero degrees from the target value, with a concentration K, and a circular uniform distribution with a probability pU. The concentration parameter, K, of the von Mises distribution captures variability in successful target retrieval (higher values reflect higher precision), and the probability of the uniform distribution, pU, reflects the likelihood of random guess responses, evenly distributed around the circular space. The probability of successful memory retrieval (pT) can be estimated as the probability of responses stemming from the target von Mises distribution ($pT = 1 - pU$). Of note, this model has previously been shown to best characterize younger adults' LTM performance in an equivalent task (Richter et al., 2016). The model was also found to fit the current data better than two alternative models: one comprising a von Mises distribution centered at the target feature value only (participants' responses reflecting variability in successful retrieval only), and the other consisting of a combination of the target von Mises distribution, uniform distribution, and von Mises distributions centered at the nontarget feature values from the same encoding display (participants' responses reflecting a mixture of variability in successful memory retrieval, guessing and binding errors), for both younger and older participants (see online supplemental materials for model comparison).
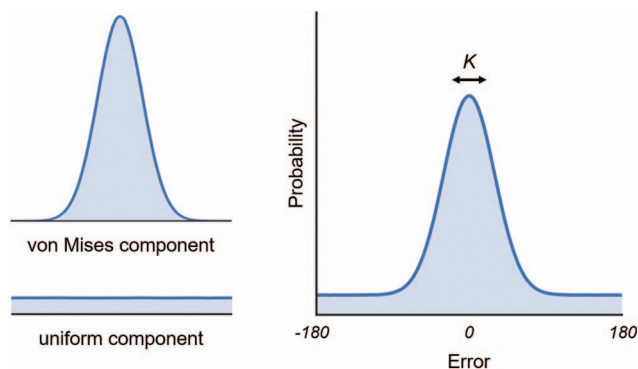
Figure 1. The probabilistic mixture model fit to participants' retrieval error data consisted of a von Mises distribution (circular equivalent of a Gaussian distribution) centered at the target feature value, and a circular uniform distribution. Success of memory retrieval was defined as the probability of responses stemming from the target von Mises distribution (pT), and precision as the concentration (K) of the von Mises distribution. See the online article for the color version of this figure.

The mixture model was fitted separately to data from each participant and task condition, yielding maximum likelihood estimates of the success (pT, probability of responses stemming from the target von Mises distribution) and precision (K, concentration of the von Mises distribution) of memory retrieval. Effects of group and task condition on the mean parameter estimates were assessed by t tests and analyses of variance (ANOVAs). For statistical analyses conducted on individual participant parameter estimates, we excluded outliers with a predefined criterion of a retrieval success (pT) or precision (K) estimate more than three standard deviations from the group mean.

We further validated the results obtained from modeling individual participants' performance by modeling performance across all trials and participants in each age group. In all experiments, the results obtained by these two approaches converged (see the online supplemental materials for aggregate analyses). Model fits were visualized with MATLAB MemToolbox (Suchow, Brady, Fougnie, & Alvarez, 2013; available at http://visionlab.github.io/MemToolbox/). Two-tailed p values are reported for all analyses. For any nonsignificant findings observed, we performed complementary Bayesian analyses to assess the strength of evidence for the null hypothesis over the alternative hypothesis. A Bayes factor (BF_{01}) of >3 in favor of the null hypothesis was interpreted as substantial evidence for the null hypothesis (Jeffreys, 1961).

Experiment 1

Experiment 1 used a continuous location report task to examine whether age-related declines in episodic memory are attributable to reduced probability of successful memory retrieval, or to reduced precision of the retrieved memory representations. Young and older participants encoded stimulus displays consisting of three everyday objects overlaid on a scene background. The location of each object on its associated background was pseudorandomly selected from a circular space, and at retrieval, participants were asked to recreate the locations of studied objects by moving the object back to its original position as accurately as they could using a continuous response dial.

Method

Participants. Twenty younger adults (19–23 years old), and 22 older adults (60–73 years old) participated in Experiment 1. One older adult participant with a precision estimate >3 SDs from the mean was excluded from the analyses, leaving 20 younger and 21 older adults to contribute to the analyses (see Table 1 for participant demographics). Older adults reported a marginally higher number of years of formal education than younger adults, $t(39) = 1.86$, $p = .070$, $d = 0.59$, $BF_{01} = 0.84$. Moreover, older adults also had higher scores than younger adults on the SILVS (Zachary & Shipley, 1986), $t(39) = 6.01$, $p < .001$, $d = 1.86$, as typically observed in studies of cognitive ageing (Verhaeghen, 2003), indicating higher crystallized intelligence in the older group.

Materials. The stimuli consisted of 180 images of distinct everyday objects and 60 images of outdoor scenes. Object and scene images were obtained from existing stimuli sets (objects: Brady, Konkle, Alvarez, & Oliva, 2008; Konkle, Brady, Alvarez, & Oliva, 2010; scenes: Richter et al., 2016) and Google image

Table 1
Participant Demographic Information in Experiment 1

| Variable	Younger adults	Older adults
n	20	21
Age	20.60 (.99)	67.14 (3.61)
Gender	12 M, 8 F	10 M, 11 F
Years of education	16.35 (1.04)	17.48 (2.50)
SILVS	32.15 (2.89)	36.52 (1.63)
MoCA	n/a	27.95 (1.16)

Note. SILVS = Shipley Institute of Living Vocabulary Scale; MoCA = Montreal Cognitive Assessment; M = males; F = females. Standard deviations reported in parentheses.

search. Three object images were randomly allocated to each scene image, forming a total of 60 trial-unique stimulus displays. The objects were each overlaid on the background scene in a location pseudorandomly selected from a 360-degree circle with a radius of 247 pixels, with a minimum distance of 62.04 degrees ensuring that the object images did not overlap on any given study display. Displays were generated once, and all participants learned the same stimuli.

Design and procedure. The location memory task consisted of 120 retrieval trials, divided into five study-test blocks (see Figure 2). In each study phase, participants viewed 12 stimulus displays for 9 s each. Participants were instructed to try and memorize the appearance of each of the displays the best they could, paying particular attention to the identity and location of each of the objects. The study phase was followed by a 30-s delay, during which participants counted backward by threes aloud, to prevent rehearsal of the studied stimuli. In the test phase, participants were first presented with a previously studied scene image with no objects overlaid on it for 9 s, during which they were instructed to think about which objects had been associated with the given scene and where they had been located. Participants were then asked to sequentially reconstruct the locations of two out of three objects that had been associated with the scene as precisely as they could (one object on the screen at a time). Each object initially appeared in a random location on the associated background, along with a response dial. Participants were able to move the object clockwise and anticlockwise around the 360-degree response dial by pressing the left and right arrow keys on the keyboard and confirmed their answer by pressing the space bar. Response time was not limited to avoid disadvantaging the older adults; however, participants were encouraged to try and respond within 15 s. The passing of 15 s was indicated by the central retrieval cue ("Location") changing color from white to red. Participants in both groups responded within the first 15 s on around 98% of trials. Participants completed 24 location retrieval trials in each block. Both encoding and retrieval trials were separated by a central fixation cross of 1 s. The order of display presentation at study and test was randomized across participants. Which two out of the three studied objects per display were selected for location retrieval, and their test order, were randomized but kept constant across participants.

Results

The distributions of participants' retrieval errors, calculated as the angular difference between the studied target feature value and
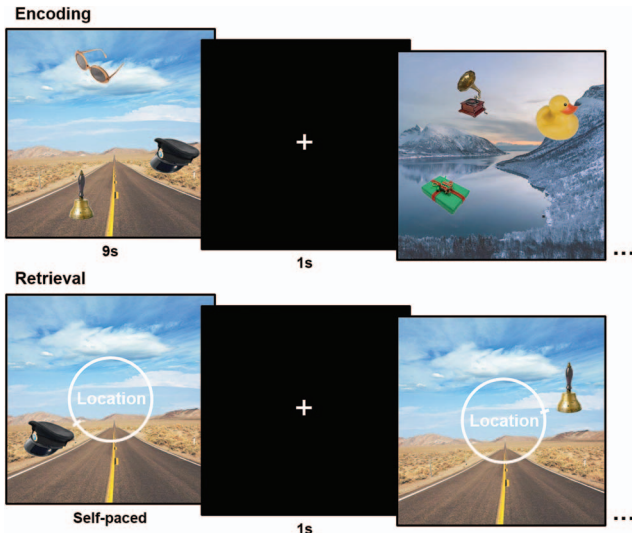
Figure 2. Example study and test trials in the location memory task in Experiment 1. Participants viewed stimulus displays (stimulus duration: 9 s) consisting of three objects overlaid on a scene background, and later recreated the locations of two objects associated with each display, by moving the object around a 360-degree response dial via keypress. Retrieval error on each trial was calculated as the angular deviation between participants' response value and the target location value (0 ± 180 degrees). See the online article for the color version of this figure.

the participant's response value, across the retrieval trials in each age group are displayed in Figure 3, illustrating that on most trials participants recalled some information about the correct location with a variable degree of noise (proportion of errors centered around the target location), but on some trials memory retrieval failed leading to participants guessing a random location on the response dial (proportion of errors distributed uniformly across the circular space).

To quantify the success and precision of memory retrieval, we fitted a probabilistic mixture model (Bays et al., 2009; Zhang & Luck, 2008) to participants' retrieval error data, yielding maxi-

mum likelihood estimates of the probability of successful memory retrieval (pT), and the precision of successful memory retrieval (K) for each participant. Examination of age differences in the model-estimated success of memory retrieval, defined as the probability of responses stemming from the von Mises distribution around the target feature value (pT), indicated no significant differences in the mean probability of retrieval success between the age groups, $t(39) = 0.43$, $p = .669$, $d = 0.13$, $BF_{01} = 3.04$ (see Figure 4A).

In contrast, the precision of memory retrieval, defined as the concentration of the target von Mises distribution (K), was significantly reduced in older adults, $t(39) = 4.96$, $p < .001$, $d = 1.55$, indicating increased variability, that is, noise, of target retrieval in the older group (see Figure 4B). To examine whether the observed age-related declines in retrieval precision were significantly greater than any age differences in retrieval success, we further converted participants' retrieval success and precision estimates to z-scores. A mixed ANOVA with the factors of memory measure (retrieval success vs. precision) and age group (young vs. old) displayed a significant interaction between age group and memory measure, $F(1, 39) = 6.00$, $p = .019$, partial $\eta^2 = 0.13$, indicating disproportionate age-related declines in retrieval precision. Age-related differences in memory performance in Experiment 1 were thus characterized by a selective deficit in the precision of memory retrieval.

Experiment 2

Following the finding of reduced precision of location memory retrieval in Experiment 1, we were next interested in exploring whether this deficit extends to the retrieval of different types of information from LTM. In younger adults, different object attributes have been shown to be independently remembered or forgotten from LTM (Brady, Konkle, Alvarez, & Oliva, 2013). Similarly, the fidelity with which different event features bound to an object are remembered has been found to be behaviorally unrelated and to rely on distinct neural circuits (Cooper & Ritchey, 2019). These findings of relative memory independence for different object features in younger adults therefore suggest scope for variability in age differences in the precision of memory retrieval
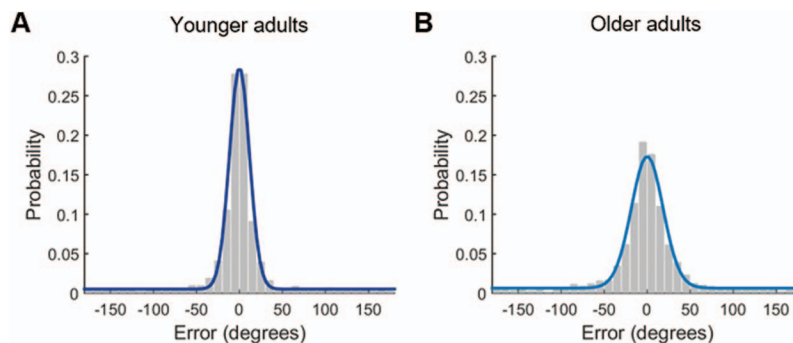
Figure 3. Distribution of retrieval errors (response feature value—target feature value) in the (A) young and (B) older adults. Colored lines (dark blue [dark grey]: younger adults, light blue [light grey]: older adults) indicate response probabilities predicted by the mixture model with target von Mises and circular uniform components (model fit to aggregate data in each group for visualization), illustrating similar retrieval success (similar height of the uniform components), but reduced memory precision in the older group (broader Gaussian component). See the online article for the color version of this figure.
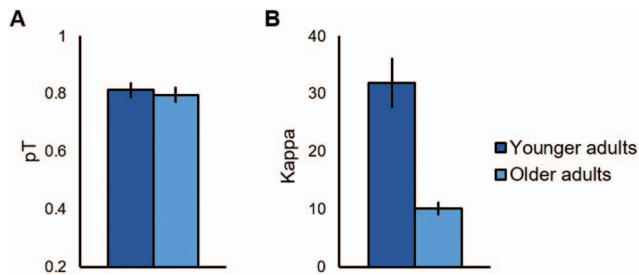
Figure 4. Mean (A) retrieval success (pT) and (B) retrieval precision (K) in each age group. Error bars display $\pm$ 1 standard error of the mean (*SEM*). See the online article for the color version of this figure.

across different object attributes. Thus, in the second experiment we aimed to assess whether the observed age-related declines in memory precision were specific to retrieval of spatial locations, or consistently observed across different object features retained in LTM.

In Experiment 2, participants encoded and retrieved stimulus displays consisting of three everyday objects that each varied in terms of their location, color and orientation in circular spaces. At test, participants recreated the appearance of each feature using the continuous response dial. We further assessed whether age-related reductions in the objective precision of memory retrieval were accompanied by age-related changes in the subjective quality of retrieved memories, by asking participants to rate the subjective vividness of their memory retrieval for each display on a continuous scale.

Method

Participants. Twenty-four younger (18–28 years old) and 24 older adults (62–79 years old) participated in Experiment 2. Two younger adults and one older adult outlier (parameter estimates >3 *SD*s from the mean) were excluded from the analyses, leaving 22 younger adults and 23 older adults to contribute to the analyses based on individual parameter estimates (see Table 2 for participant demographics). Six of the older adults had also participated in Experiment 1 (no overlap in task stimuli). No significant differences in memory performance (mean absolute retrieval error across trials) were detected between these six participants and the remaining older adults, $t(21) = 1.44$, $p = .165$, $BF_{01} = 1.21$. The older adults reported a significantly higher number of years of formal education than younger adults, $t(43) = 2.66$, $p = .011$, $d = 0.80$, and scored on average higher on the SILVS (Zachary & Shipley, 1986), $t(42) = 4.20$, $p < .001$, $d = 1.26$.

Materials. Stimuli for the continuous report task in Experiment 2 consisted of 120 images of distinct everyday objects and 40 images of textured backgrounds. The object images were obtained from an existing stimuli set (Brady et al., 2013, available at http://timbrady.org/stimuli/ColorRotationStimuli.zip), and the background images from Google Image Search (no overlap with Experiment 1). Objects with rotational symmetry were excluded from the stimuli. The stimuli were randomly allocated to form a total of 40 trial-unique study displays each consisting of three objects overlaid on a texture background. In contrast to Experiment 1, in Experiment 2 the objects on each display varied along

three perceptual features: location, color and orientation. Values for each of these features were pseudorandomly drawn from a circular space (0–360 degrees) with the constraint of a minimum distance of 62.04 degrees between two features of the same type on each display. As in Experiment 1, this minimum distance was required to create nonoverlapping object locations, and for consistency also applied to the other two feature dimensions. All participants learned the same displays.

Design and procedure. The continuous report task consisted of 10 study-test blocks (see Figure 5). In each study phase, participants sequentially viewed four stimulus displays (stimulus duration: 12 s) and were instructed to memorize each display the best they could, including both the background image and the identity and appearance (location, color and orientation) of each of the objects. In the test phase, participants were first asked to rate the vividness of their memory for each display, and to base this vividness judgment on how vividly they could recall the appearance of all of the three objects associated with that display. Participants were presented with the background image only, along with a question "How vividly do you remember this display?" in the center of the image. After 2-s delay a response scale was added and participants could indicate the vividness of their memory by moving a slider on a 100-point continuous scale from 0 (*not vivid*) to 100 (*very vivid*). After the vividness rating, participants sequentially reconstructed the features (location, color, and orientation) of two out of three objects on each display. For feature retrieval, the test object initially appeared in a randomly allocated location, color, and orientation on the associated background along with the response dial. A central cue noted the feature being tested ("Location," "Color," or "Orientation"), and after responding to one of the feature questions, participants' reconstruction of that feature's appearance remained unchanged for the following feature questions for the same object. As in Experiment 1, the test phase was self-paced, but participants were encouraged to respond within 15 s. The study and test trials were separated by a fixation cross of jittered duration (400 ms to 2,500 ms, $M = 1,025$ ms), and the study and test phases by a 10-s delay.

Participants completed 40 vividness trials, and 240 feature retrieval trials (80 per feature) in total. The order of display presentation at study and test was randomized across participants. Selection of two objects from each display for feature retrieval and their test order was randomized but kept constant across participants. The order of feature questions for each object was pseudorandomized across participants with the constraint of no individual

Table 2

Participant Demographic Information in Experiment 2

Variable	Younger adults	Older adults
n	22	23
Age	20.95 (2.46)	71.91 (4.65)
Gender	12 M, 10 F	12 M, 11 F
Years of education	16.05 (1.43)	17.83 (2.81)
SILVS[a]	33.77 (3.66)	37.41 (1.76)
MoCA	n/a	28.22 (1.17)

Note. SILVS = Shipley Institute of Living Vocabulary Scale; MoCA = Montreal Cognitive Assessment; M = males; F = females. Standard deviations reported in parentheses.
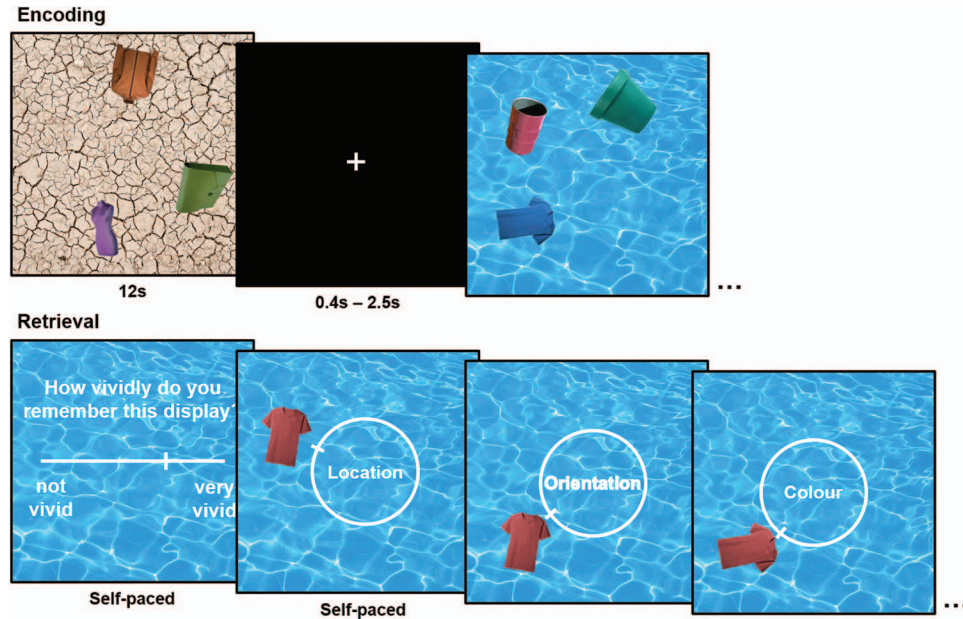[a] SILVS score missing for one older adult due to experimenter error.

Figure 5. In Experiment 2, participants studied stimulus displays consisting of three objects varying along three features: location, color and orientation (stimulus duration: 12 s). For each display, participants first rated the vividness of their memory retrieval, and then recreated the features of two out of three objects on each display, using the continuous response dial. See the online article for the color version of this figure.

feature tested more than four consecutive times in the same sequential position (i.e., first, second, or third), and with each feature tested 26–28 times in each position.

Results

Distributions of retrieval errors in each feature condition and age group in Experiment 2 are displayed in Figure 6. A mixed ANOVA with the factors of feature (location, color, orientation) and age group (young vs. old) yielded no significant main effect of age group, $F(1, 43) = 2.29$, $p = .138$, partial $\eta^2 = 0.05$, $BF_{01} = 1.63$, but a significant effect of feature, $F(2, 86) = 85.26$, $p < .001$, partial $\eta^2 = 0.67$. Importantly, there was a significant interaction between age group and feature condition, $F(2, 86) = 5.03$, $p = .009$, partial $\eta^2 = 0.11$, indicating that age differences in retrieval success varied across the three feature conditions (see Figure 7A). No significant age differences in retrieval success were observed in the location, $t(43) = 0.13$, $p = .901$, $d = 0.04$, $BF_{01} = 3.37$, or color, $t(43) = 1.34$, $p = .186$, $d = 0.40$, $BF_{01} = 1.64$, conditions. However, the older adults exhibited significantly lower probability of successful memory retrieval than younger adults in the orientation condition, $t(43) = 2.45$, $p = .018$, $d = 0.73$. The orientation condition had the lowest retrieval success out of the three feature conditions in the younger adults (lower retrieval success than color, $t(21) = 4.17$, $p < .001$, $d = 0.89$, and location, $t(21) = 8.01$, $p < .001$, $d = 1.71$), indicating that the only significant age differences in retrieval success were observed for the condition that participants in the younger group appeared to find the most difficult.

In contrast, for retrieval precision, a mixed ANOVA with the factors of feature (location, color, orientation) and age group (young vs. old) displayed a significant main effect of age group,

$F(1, 43) = 11.54$, $p = .001$, partial $\eta^2 = 0.21$, indicating reduced precision of memory retrieval in the older group (see Figure 7B). Age differences in retrieval precision did not vary significantly across the feature conditions, $F(2, 86) = 0.14$, $p = .872$, partial $\eta^2 = 0.00$, $BF_{01} = 7.28$, indicating a comparable degree of age-related loss of mnemonic precision across different object features retained in LTM.

We next compared the magnitude of age differences in retrieval success and precision for each feature condition with a separate mixed ANOVA with the factors of measure (retrieval success vs. precision) and age group (young vs. old). We observed a significant interaction between age group and memory measure in the location condition, $F(1, 43) = 5.52$, $p = .023$, partial $\eta^2 = 0.11$, but not in the color, $F(1, 43) = 0.17$, $p = .679$, partial $\eta^2 = 0.00$, $BF_{01} = 3.51$, or orientation, $F(1, 43) = 0.33$, $p = .570$, partial $\eta^2 = 0.01$, $BF_{01} = 2.91$, conditions (estimates of retrieval success and precision z-scored), thus providing evidence for a significantly disproportionate age-related deficit in retrieval precision in the location condition only.

Furthermore, despite reductions in the objective precision of memory retrieval, the mean subjective ratings of memory vividness did not significantly differ between the age groups, $t(43) = 0.71$, $p = .485$, $d = 0.21$ $BF_{01} = 2.77$, with both age groups rating their memory retrieval as moderately vivid (younger: $M = 45.09$, $SD = 13.12$, older: $M = 49.65$, $SD = 27.42$, on a scale 0–100). Mean memory vividness did not significantly correlate with the success (younger: $r = .23$, $p = .313$, $BF_{01} = 2.35$; older: $r = -.06$, $p = .791$, $BF_{01} = 3.74$) or precision (younger: $r = .15$, $p = .507$, $BF_{01} = 3.08$; older: $r = .07$, $p = .748$, $BF_{01} = 3.69$) of memory retrieval estimated across the feature conditions in either age group.
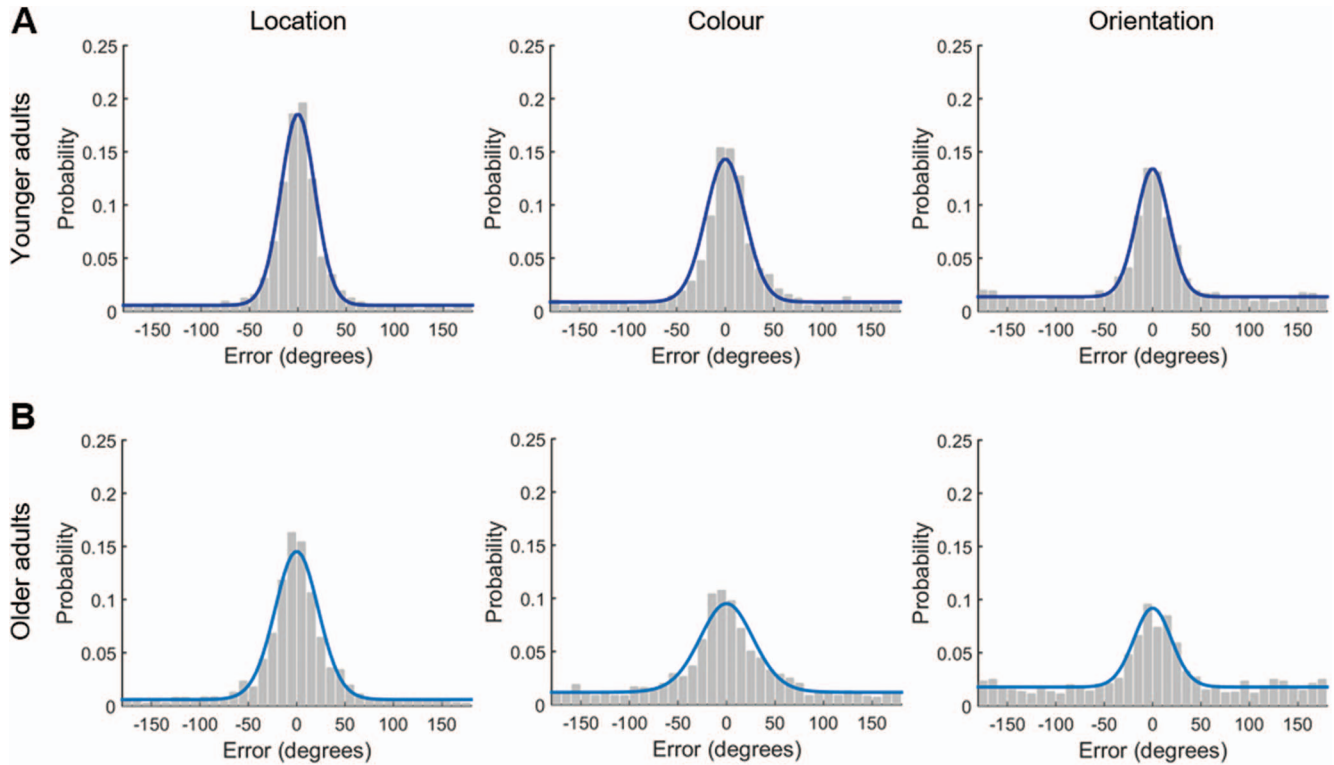
Figure 6. Distribution of retrieval errors in each feature condition in the (A) younger and (B) older adults. Colored lines (dark blue [dark grey]: younger adults, light blue [light grey]: older adults) illustrate response probabilities predicted by the mixture model (model fit to aggregate data for visualization). See the online article for the color version of this figure.

Discussion

In Experiment 2, we assessed the fidelity of participants' LTM retrieval for three different object features: location, color and orientation. Consistent with results from the location memory task in Experiment 1, we here observed significant age-related declines in the precision of episodic retrieval across the features tested, indicating consistent age-related declines in memory fidelity across different types of information retained in LTM. In contrast to Experiment 1, in the present experiment we also observed a

significant age-related reduction in retrieval success in the orientation condition. This was also the condition resulting in lowest retrieval success out of the three feature conditions in the younger adults (see Cooper et al., 2017 for similar results), potentially suggesting an influence of task difficulty. However, it should be noted that although our complementary Bayesian analyses provided substantial evidence for age-invariant success of memory retrieval in the location condition, considerable support for this null hypothesis was not observed in the color condition. Despite
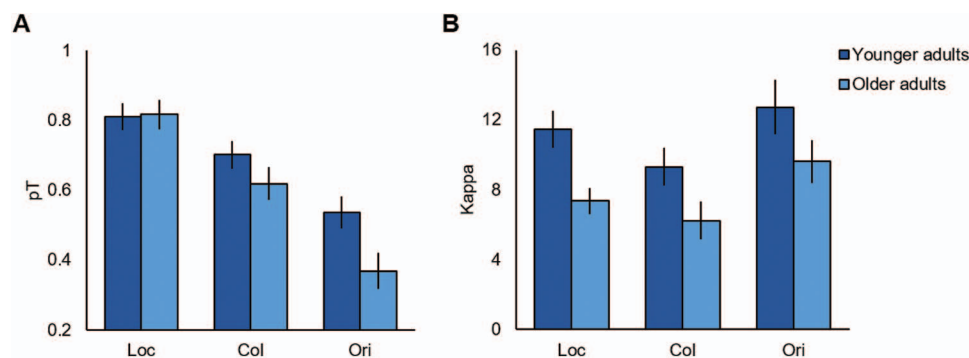

Figure 7. Mean (A) retrieval success (*pT*) and (B) retrieval precision (*K*) in each age group and feature condition (Loc = location, Col = color, Ori = orientation). Error bars display ± 1 *SEM*. See the online article for the color version of this figure.

reductions in objective measures of performance, the older adults did not display decreases in the subjective vividness of their memory retrieval, consistent with previous reports of lack of age-related decline in memory vividness (Johnson, Kuhl, Mitchell, Ankudowich, & Durbin, 2015; St-Laurent et al., 2014).

Experiment 3

Experiments 1 and 2 both revealed age-related deficits in the precision of episodic memory retrieval, however it is unclear how specific these decreases are to LTM, or whether they might at least partly reflect age-related declines in the fidelity of information processed at the level of perception or WM. As the precision of mnemonic representations is constrained by the fidelity of sensory inputs (Ma, Husain, & Bays, 2014), age-related reductions in perceptual processing might contribute to the loss of memory precision observed in the current experiments, consistent with the information degradation hypothesis of age-related cognitive decline (Monge & Madden, 2016). Alternatively, or additionally, age-related limitations in episodic memory precision might arise from decreases in the precision of WM, documented in previous studies (Peich et al., 2013; Pertzov et al., 2015). Previous work in younger adults has proposed LTM and WM to exhibit similar constraints on representational fidelity (Brady et al., 2013), supporting the hypothesized link between age-related decreases in the precision of WM and LTM.

The aim of the third experiment was therefore to examine whether age-related declines in the precision of episodic memory could be partially, or fully, explained by declines in the fidelity of perceptual and/or WM representations. Participants completed perceptual, WM, and LTM versions of the continuous report task for object color. Color was chosen as the tested feature in this experiment as previous research in younger adults employing a similar task has found color to be a sufficiently sensitive feature for

investigating the fidelity of all three cognitive functions: perception, WM, and LTM (Brady et al., 2013).

Method

Participants. Twenty-six younger (18–30 years old) and 24 older adults (60–82 years old) took part in Experiment 3. Two younger adults were excluded from the experiment prior to data analysis, one due to a counterbalancing error leading to the participant completing the same tasks twice, and one due to failure to attend the second study session. Furthermore, two younger and two older adult outliers (parameter estimates >3 SDs from the group mean) were excluded from the analyses based on individual participant parameter estimates, leaving 22 younger and 22 older adults to contribute to the analyses (see Table 3 for participant demographics). Similar to previous experiments, older adults reported a significantly higher number of years of formal education than younger adults, $t(42) = 2.70$, $p = .010$, $d = 0.82$, and scored significantly higher on the SILVS (Zachary & Shipley, 1986), $t(42) = 6.91$, $p < .001$, $d = 2.08$.

Materials. Stimuli for all tasks consisted of 540 everyday objects (Brady et al., 2008, 2013), including the object stimuli from Experiment 2 (no overlap in participants). Objects that were not readily color-rotated were initially converted to the same hue of red as the Brady et al. (2013) color-rotated object stimuli with Matlab scripts available at https://bradylab.ucsd.edu/stimuli.html. Object images were randomly allocated to each task type, with 120 objects allocated to the LTM task, 360 to the WM task, and 60 to the perceptual task. In the LTM and WM tasks, stimulus displays consisted of three distinct objects overlaid on a gray background. To keep the amount of visual input consistent across tasks, stimulus displays in the perception task also comprised three objects overlaid on a gray background. However, as this task involved no demands on memory, three versions of the same object were used.

Table 3
Participant Demographic and Neuropsychological Test Data in Experiment 3

Variable	Younger adults	Older adults	p value
n	22	22	—
Age	22.55 (3.54)	69.09 (6.12)	—
Gender	6 M, 16 F	4 M, 18 F	—
Years of education	16.36 (2.65)	19.07 (3.87)	.010
SILVS	32.55 (3.73)	38.41 (1.40)	<.001
MoCA	n/a	28.14 (1.25)	—
Trails A (s)	36.68 (28.30)	50.41 (20.41)	.072
Trails B (s)[a]	68.35 (32.72)	79.52 (25.80)	.231
Rey-Osterrieth complex figure copy	34.86 (1.32)	34.80 (1.47)	.872
Rey-Osterrieth complex figure immediate	24.82 (5.53)	19.20 (7.59)	.008
Rey-Osterrieth complex figure delayed	24.66 (6.33)	19.27 (7.40)	.013
Verbal paired associates immediate	27.91 (4.37)	23.00 (6.91)	.007
Verbal paired associates delayed	7.91 (.43)	7.23 (1.23)	.018
Letter fluency	49.86 (10.29)	55.18 (10.21)	.093
Digit span forward	12.23 (2.31)	11.05 (2.84)	.137
Digit span backward	8.59 (2.58)	8.00 (2.18)	.416

Note. SILVS = Shipley Institute of Living Vocabulary Scale; MoCA = Montreal Cognitive Assessment; M = males; F = females. Standard deviations reported in parentheses. *p* values for independent samples *t* tests comparing younger and older adults.
[a] Scores on the Trail making B task excluded from two younger, and one older participant due to experimenter error.

The color and location of the objects in each display were pseudorandomly chosen from circular parameter spaces with the minimum constraint of 62.04 degrees between two feature values of the same type. A total of 40 unique stimulus displays were created for the LTM task, 120 for the WM task, and 60 for the perception task. All participants viewed the same displays.

Design and procedure. Participants attended two testing sessions, with a minimum 1-week delay between the sessions (delay for younger adults $M = 11.45$ days, $SD = 6.57$, older adults $M = 10.82$ days, $SD = 7.05$, no significant difference between the groups, $t(42) = 0.31$, $p = .758$, $d = 0.09$, $BF_{01} = 3.23$). In addition to the three color report tasks, participants completed a battery of standard neuropsychological tasks including measures of verbal (Verbal Paired Associates, WMS-III; Wechsler, 1997b) and nonverbal memory (Rey-Osterrieth Complex Figure test; Osterrieth, 1944), executive function (Verbal fluency, Trails A & B; Delis, Kaplan, & Kramer, 2001), and WM (Digit span forward and backward, WAIS-III; Wechsler, 1997a). Participants' performance on the neuropsychological tasks is presented in Table 3. The assignment of the color report tasks and neuropsychological tests to each testing session was counterbalanced across participants, with the memory versions of the task completed in separate sessions.

Color report tasks. During the test phase of each of the continuous report tasks, the target object initially appeared in a randomly allocated color but in its studied location and orientation (memory for location or orientation not tested in Experiment 3). As in the previous experiments, response time in the test phase was not limited in any of the tasks, but participants were encouraged to respond within 15 s. Trials in each task were separated by a 1-s central fixation cross. The order of displays at study and test was randomized across participants. The order of the objects to test per display in the LTM task (three objects tested for each display), and the selection of objects to test per display in the WM and perceptual tasks (one object tested for each display) was randomized but kept constant across participants.

The LTM task consisted of 120 color retrieval trials, divided into eight study-test blocks (see Figure 8). In each study phase, participants sequentially viewed five stimulus displays (stimulus duration: 9 s). Participants were instructed to try and memorize the identity and color of each object the best they could. The study phase was followed by a 30-s delay filled with counting backward by threes aloud, to prevent rehearsal of the studied stimuli and to ensure that the task relied on LTM. In the test phase, participants recreated the colors of all the objects studied in the preceding block (15 retrieval trials per block).

In the WM task, participants also completed 120 color retrieval trials in total, divided into eight blocks of 15 trials each (see Figure 8). In this task, participants studied only one stimulus display at a time (stimulus duration: 3 s). To prevent reliance on sensory memory, display presentation was followed by presentation of a colored mask image for 100 ms, followed by a 900-ms central fixation cross. After the total delay of 1 s, participants reconstructed the color of one of the objects from the preceding display. Participants were only tested on one object per display to ensure consistent demands on WM.

The perceptual task included 60 trials, divided into two blocks of 30 trials each (see Figure 8). On each trial, participants saw two displays side-by-side on the screen. One of the displays had three versions of the same object presented in different colors. The other display had only one object, the color of which participants were able to adjust with the response dial. The participants' task was to match the color of the test object to the color of an object in the same relative location on the other display, surrounded by a white square. As the display was simultaneously in view, this task placed minimal demands on memory. The side of presentation of the display and test object on each trial (left vs. right) was randomized across participants.

Results

As in both of the memory tasks, errors in the perception task were calculated as the angular deviation between participants' response value and the target color value (0 ± 180 degrees). Distributions of errors in each task and age group are displayed in Figure 9.

Focusing first on LTM, comparison of mean parameter estimates indicated no significant differences in the probability of successful LTM retrieval between the age groups, $t(42) = 0.76$, $p = .454$, $d = 0.23$, $BF_{01} = 2.67$, but a significant decline in memory precision in the older group, $t(42) = 4.12$, $p < .001$, $d = 1.24$ (see Figures 10A and 10B). The deficit in LTM precision was disproportionate to any age differences in LTM retrieval success as indicated by a significant interaction between the factors of memory measure (retrieval success vs. precision) and age group (young vs. old) in a mixed ANOVA, $F(1, 42) = 4.26$, $p = .045$, partial $\eta^2 = 0.09$ (retrieval success and precision estimates z-scored). Similarly, in WM, we observed no significant age differences in the probability of successful memory retrieval, $t(42) = 0.80$, $p = .428$, $d = 0.24$, $BF_{01} = 2.60$, but the older group displayed a significant reduction in memory precision, $t(42) = 3.12$, $p = .003$, $d = 0.94$ (see Figures 10A and 10B). However, the evidence for a disproportionate deficit in memory precision in the WM task was not significant, $F(1, 42) = 2.15$, $p = .150$, partial $\eta^2 = 0.05$, $BF_{01} = 1.13$ (estimates z-scored). Lastly, the age groups did not differ significantly in terms of the probability of reporting the correct target color in the perception task, $t(42) = 1.70$, $p = .097$, $d = 0.51$, $BF_{01} = 1.07$ (see Figure 10A), during which the stimulus display was simultaneously in view as the participants selected their response. However, even in the perceptual task, older adults were significantly less precise at matching the color of the objects than younger adults, $t(42) = 3.40$, $p = .001$, $d = 1.03$ (see Figure 10C). The evidence for a disproportionate deficit in precision in the perceptual task was not significant, $F(1, 42) = 1.33$, $p = .256$, partial $\eta^2 = 0.03$, $BF_{01} = 1.82$ (estimates z-scored).

To investigate whether variation in perception or WM predicted LTM performance in each of the age groups, we used linear regression (see Figure 11). In each age group separately, we examined whether perceptual precision or WM precision alone, or a combination of these two variables, predicted the precision of LTM. In younger adults, a model including both perceptual and WM precision as predictor variables did not significantly predict the precision of LTM retrieval, $R^2 = .12$, $F(2, 19) = 1.24$, $p = .311$, $BF_{01} = 2.22$, nor did either of these two variables alone (perception: $R^2 = .11$, $F(1, 20) = 2.54$, $p = .126$, $BF_{01} = 1.07$; WM: $R^2 = .01$, $F(1, 20) = 0.14$, $p = .717$, $BF_{01} = 2.48$). In contrast, in the older group, a model including both perceptual and WM precision was a significant predictor of LTM precision, $R^2 =$
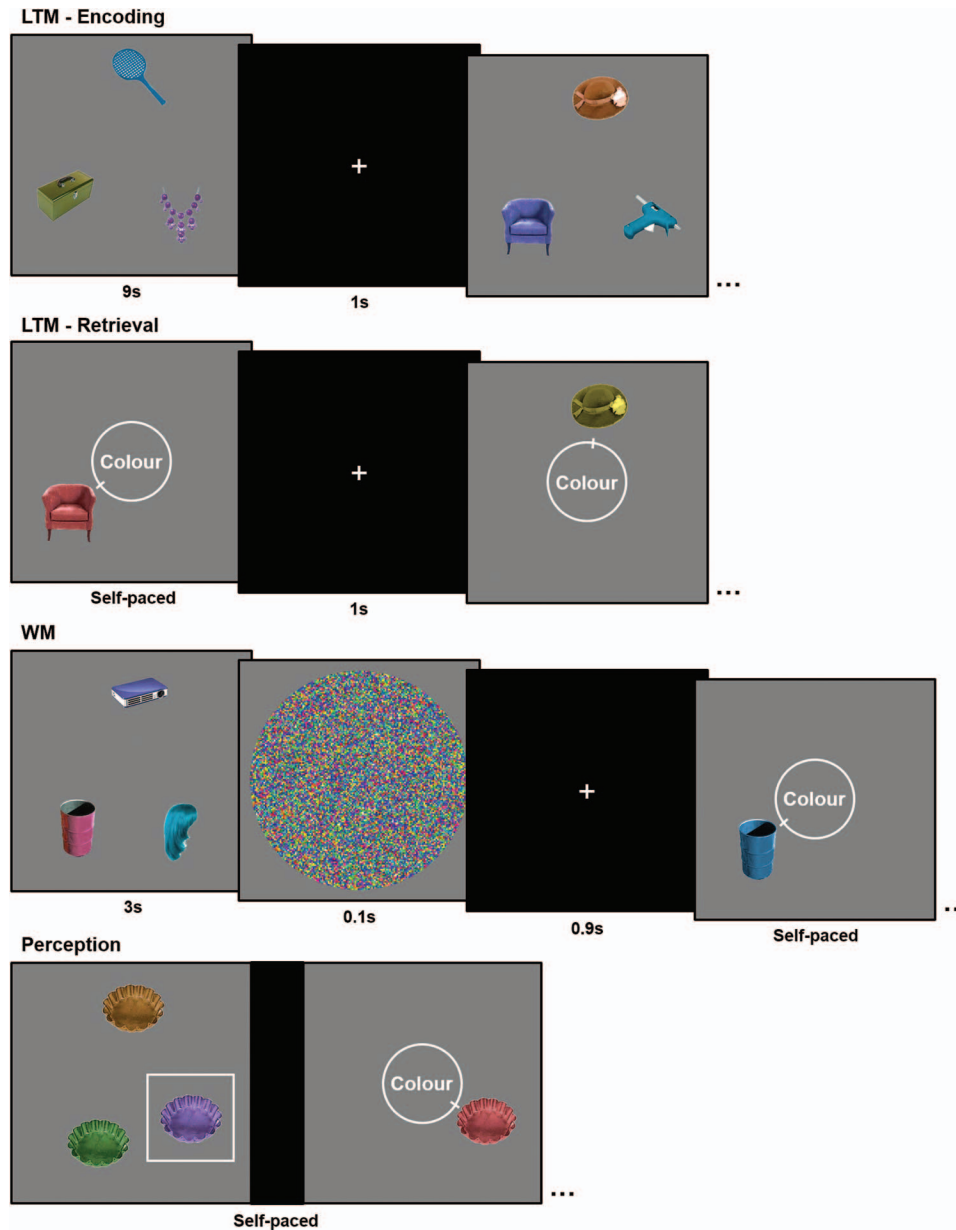
Figure 8. Example trials in each of the three color report tasks. In the long-term memory (LTM) task participants studied five stimulus displays in a row (9 s each), before retrieving the colors of all objects after a 30-s delay. In the working memory (WM) task, participants studied one stimulus display at a time (3 s each) and retrieved the color of one object after 1-s delay. In the perception task, participants matched the color of one object per display while the stimulus display was simultaneously in view. See the online article for the color version of this figure.

.36, $F(2, 19) = 5.45$, $p = .014$. This result was driven by a significant effect of WM precision on LTM precision, $R^2 = .35$, $F(1, 20) = 10.67$, $p = .004$, whereas perceptual precision alone did not significantly predict LTM precision in the older group, $R^2 = .12$, $F(1, 20) = 2.68$, $p = .117$, $BF_{01} = 1.03$. To examine whether the relationship between WM precision and LTM precision significantly differed between the age groups, we further computed a cross-group regression analysis of LTM precision with the predictors of age group and WM precision. The interaction term between age group and WM precision was not significant in this model however, $t(40) = 1.03$, $p = .307$, $BF_{01} = 1.65$, therefore not providing evidence for a significantly different relationship between WM and LTM precision between the age groups.

We additionally observed a trend for perceptual precision to predict WM precision in both the younger, $R^2 = .15$, $F(1, 20) = 3.60$, $p = .072$, $BF_{01} = 0.76$, and older adults, $R^2 = .15$, $F(1, 20) = 3.41$, $p = .080$, $BF_{01} = 0.81$. Similarly a trend for a relationship between the success of WM and LTM retrieval was
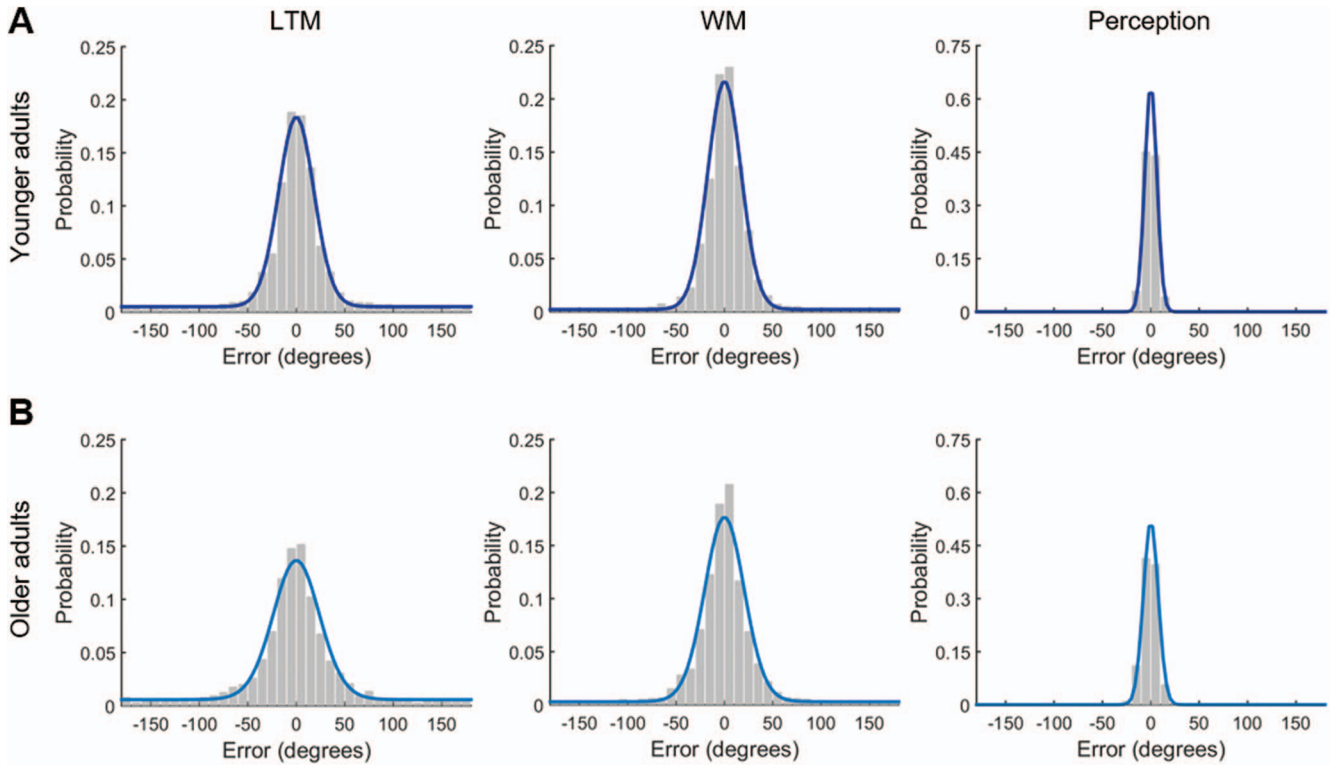
Figure 9. Distribution of errors in the long-term memory (LTM), working memory (WM), and perception color report tasks in (A) younger and (B) older adults. Colored lines (dark blue [dark grey]: younger adults, light blue [light grey]: older adults) illustrate response probabilities predicted by the mixture model (model fit to aggregate data for visualization). Note the different scaling of the y-axes for the perception task. See the online article for the color version of this figure.

evident in the young, $R^2 = .16$, $F(1, 20) = 3.68$, $p = .069$, $BF_{01} = 0.74$, but not in the older group, $R^2 = .00$, $F(1, 20) = 0.05$, $p = .825$, $BF_{01} = 2.56$. The success of WM retrieval was not significantly related to LTM precision (young: $R^2 = .01$, $F(1, 20) = 0.15$, $p = .705$, $BF_{01} = 2.47$; old: $R^2 = .01$, $F(1, 20) = 0.16$, $p = .698$, $BF_{01} = 2.46$) in either age group. Note that we did not examine the relationship between probability of successful target reports in the perceptual task and other performance measures due to lack of

variability on this measure in both age groups (younger adults $M = 1.00$, $SD = 0.01$, older adults $M = 0.99$, $SD = 0.01$).

With WM precision accounting for 35% of variance in the precision of LTM retrieval in the older group, we next examined whether the age-related deficits in LTM precision persisted after controlling for the age-related reductions in the precision of WM retrieval. Critically, after controlling for variability in WM precision, $F(1, 41) = 10.23$, $p = .003$, partial $\eta^2 = .20$, and after controlling for variability

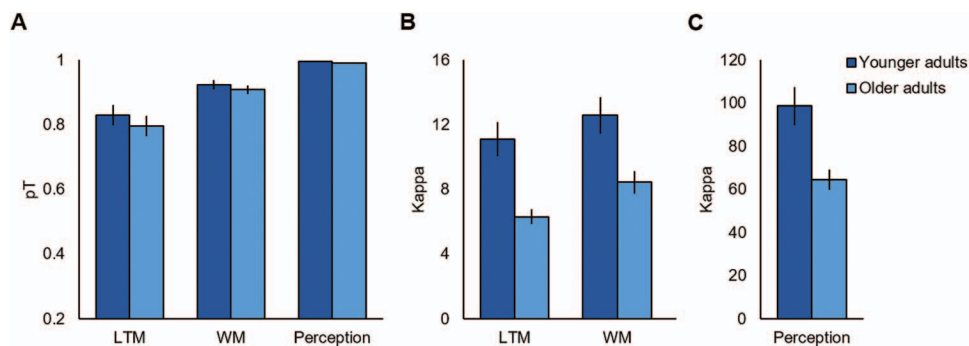*Figure 10.* A, B: Mean probability of target reports (*pT*), and B, C: precision (*K*) in each task and age group. Note that precision in the perceptual task is plotted separately due to higher *K* values in this task. Error bars display ± 1 *SEM*. See the online article for the color version of this figure.
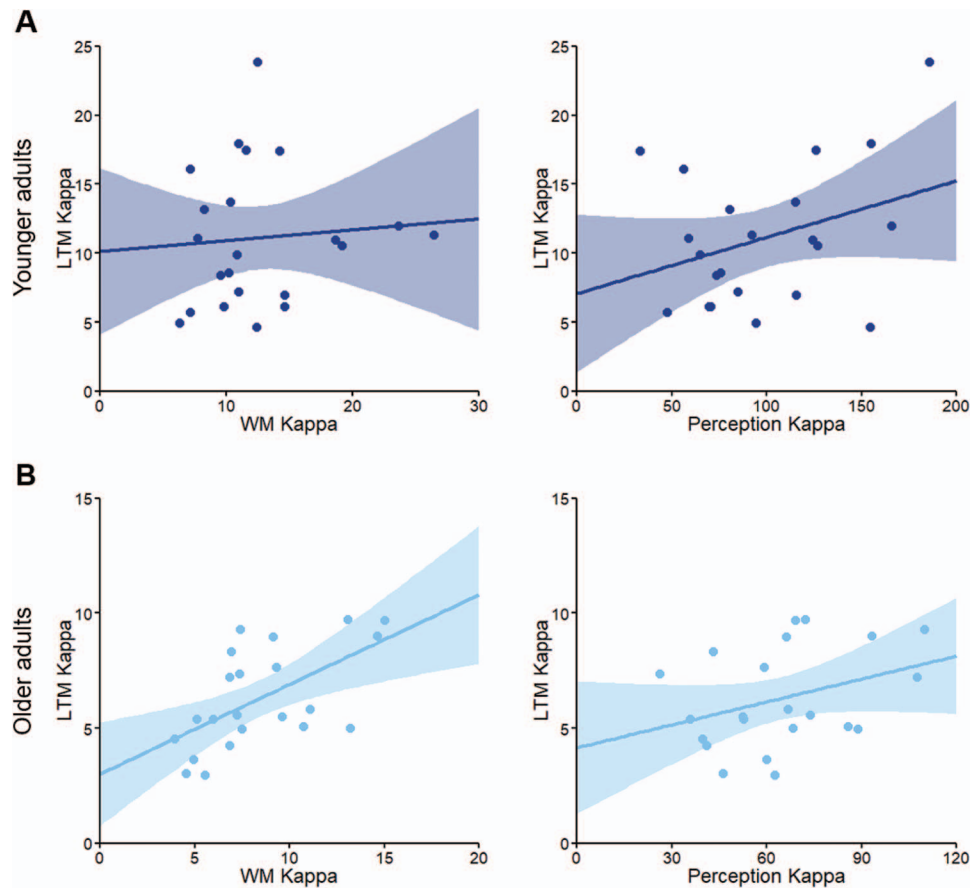
Figure 11.   Relationship between long-term memory (LTM) and working memory (WM) precision, and LTM and perceptual precision in the (A) younger and (B) older groups. Note the different scaling of axes between the age groups. See the online article for the color version of this figure.

in both WM and perceptual precision, $F(1, 40) = 6.41$, $p = .015$, partial $\eta^2 = .14$, in an analysis of covariance, we still observed significant age-related declines in the precision of LTM retrieval.

Discussion

In Experiment 3, we examined the degree to which age-related changes in the fidelity of perception and/or WM might contribute to the observed age-related deficits in episodic memory precision. Consistent with Experiments 1 and 2, the precision of LTM retrieval exhibited significant age-related declines in the current experiment. In addition to LTM, precision reductions were further evident in the older group at the level of perception and WM. In contrast, the probability of successful target reports did not exhibit significant age differences in any of the three tasks. However, the Bayes factor analyses failed to provide substantial evidence in favor of the null hypothesis of age-invariant probability of successful target reports in the current experiment; therefore the selectivity of precision deficits in the current tasks remains unclear.

We next assessed the extent to which variability in LTM precision might be attributable to variation in perceptual and/or WM precision. In the older adults, a significant relationship between WM precision and LTM precision was observed, suggesting a contribution

of decreases in the fidelity of WM to the deficit in LTM precision observed in the older group. Perceptual precision on the other hand did not account for a significant proportion of variance in the precision of LTM in the older or younger adults. The Bayes factor analyses indicated only weak evidence for these null relationships however, such that we cannot exclude the possibility that variability in perceptual precision may have also contributed to variability in the precision of LTM. Importantly, we still observed significant age-related declines in the precision of LTM after controlling for variability in the precision of both perception and WM. This result indicates that the observed age-related reductions in LTM precision could not fully be accounted for by differences in the fidelity of information processed at lower levels. Furthermore, controlling for performance in the perceptual task, in which the response format was identical to that of the memory tasks, also accounted for any potential influence of age differences in sensorimotor accuracy to the differences in episodic memory precision observed in the older group.

General Discussion

Declines in episodic memory retrieval are consistently observed with healthy ageing (Grady, 2012; Hedden & Gabrieli, 2004; Nyberg et al., 2012). Although a wealth of studies has investigated

the effects of ageing on the success of episodic memory retrieval (e.g., Cansino et al., 2018; Koen & Yonelinas, 2014; Simons, Dodson, Bell, & Schacter, 2004), less is known about whether ageing may also affect the fidelity of retrieved memories (Nilakantan et al., 2018). In the current study, we sought to better characterize the nature of age-related declines in episodic memory retrieval by distinguishing whether age-related changes reflect reduced probability of successfully retrieving information from memory, and/or decreased precision of the retrieved memory representations. In three experiments, we consistently observed age-related reductions in the precision of episodic memory retrieval. These declines in mnemonic precision were evident across different types of information retrieved from LTM (object location, color, and orientation), and persisted after controlling for age-related reductions in the fidelity of perception and WM. In contrast to memory precision, significant age-related decreases in the probability of successful memory retrieval were observed only in the orientation condition in Experiment 2, and not elsewhere. This was also the condition resulting in the lowest retrieval success in the younger group, suggesting an effect of task difficulty. Together, these results highlight reduced precision of memory representations as one factor contributing to age-related episodic memory impairments and suggest that the success and precision of episodic recollection might be differentially sensitive to age-related cognitive decline.

The current findings of decreased memory precision in older age are consistent with previous proposals of age-related reductions in the quality, and specificity, of memory representations (Burke et al., 2018; Goh, 2011; Li et al., 2001; Trelle, Henson, Green, & Simons, 2017). However, where previous behavioral investigations have often relied on subjective judgments or on categorical measures of memory success to draw inferences about age-related changes in memory quality, the current paradigm provided a more direct behavioral measure of memory fidelity, unconfounded by age-related changes in the success of memory retrieval. In the current experiments, we observed consistent age-related declines in memory precision across different object features (location, color and orientation) stored in LTM. These results suggest that decreases in memory precision may be a consistent feature of age-related memory decline, and not specific to the type of material tested. Indeed, such material-independent declines would be predicted by previous accounts proposing increases in neural noise to limit the fidelity of memory representations in older age (Li et al., 2001; Welford, 1958, 1981).

In contrast to memory precision, significant age-related decreases in the probability of successful memory retrieval were detected in the current experiments only in the orientation condition of Experiment 2. This relative sparing of retrieval success in older age is consistent with the notion that while memory for the gist of an event or stimulus might be preserved in ageing, the more fine-grained details tend to be lost (Dennis et al., 2007, 2008; Kensinger & Schacter, 1999; Nilakantan et al., 2018). Other previous studies have demonstrated robust age-related declines in the success of episodic recollection, however (e.g., Cansino et al., 2018; Simons et al., 2004). This apparent discrepancy between the current results and previous findings may be partially explained by age-related decreases on categorical measures of memory success in previous studies being at least to some extent attributable to reduced fidelity of the underlying memory representations, rather

than a failure to retrieve the representations per se (Nilakantan et al., 2018). For instance, a failure to discriminate between two similar sources of memories, such as between two female or two male voices (Simons et al., 2004), could result from a noisier memory representation of the source, leading to selection of the incorrect retrieval response, and thereby reduced retrieval success.

However, it should be noted that the Bayes factor analyses provided substantial evidence in favor of age-invariant probability of successful memory retrieval only in the location conditions of Experiment 1 and 2. Although no significant differences in the probability of successful memory retrieval were detected in the color conditions of Experiment 2 and 3 either, numerically the success of memory retrieval was observed to be lower in the older group in these conditions. It therefore remains to be clarified how selective the memory precision deficits in older age are. The finding that age-related declines in memory precision were observed even when retrieval success was matched between the age groups, and that these declines were often disproportionate to any age differences in retrieval success, as indicated by an interaction between memory measure and age group in location conditions in Experiment 1 and 2 and the LTM task in Experiment 3, suggests that memory precision may be more sensitive to age-related cognitive decline. However, longitudinal evidence is required to establish the rate of change in each of these two aspects of memory retrieval.

Age-related changes in retrieval success were observed in the current study in the orientation condition only, which may reflect the relatively high task difficulty of this condition (as indicated by lower retrieval success in this condition in comparison to the location and color conditions in the younger group), rather than an impairment specific to the retrieval of object orientations. Indeed, previous evidence from younger adults using a similar paradigm has also demonstrated orientation to be the most difficult condition out of the three object features (Cooper et al., 2017). Emergence of age-related decreases in the probability of successful memory retrieval with increased task difficulty is consistent with the notion of exaggerated age difference in cognitive performance with increased task demands (Reuter-Lorenz & Cappell, 2008). These findings suggest that although the success of memory retrieval may remain at a level similar to the young in the older group when task demands are relatively low, multiple aspects of memory retrieval might begin to break down when task demands are increased. However, given that task difficulty was confounded with feature condition in the current experiment, future research employing different difficulty manipulations on the same feature condition is required to distinguish between feature-based and task difficulty-based interpretations.

In Experiment 3, we further sought to evaluate how specific the observed age-related declines in memory precision were to LTM. One concern when investigating age-related memory reductions is that observed differences might be a direct consequence of more general cognitive decline with age, including decreased perceptual abilities (Baltes & Lindenberger, 1997; Lindenberger & Baltes, 1994), or WM function (Brockmole & Logie, 2013; Salthouse & Babcock, 1991). In Experiment 3, we assessed whether any age-related declines in the fidelity of perception or WM might account for the age-related deficit observed in the precision of LTM. Interestingly, we observed significant age-related declines in the representational fidelity of all three cognitive functions: percep-

tion, WM and LTM. The fidelity of WM retrieval was a significant predictor of LTM precision in the older group, suggesting that age-related declines in the fidelity of WM contribute to declines in the precision of LTM representations. This is consistent with previous reports highlighting the importance of WM processes for successful LTM encoding (Blumenfeld & Ranganath, 2006; Khader, Jost, Ranganath, & Rösler, 2010), as well as findings implicating WM as a predictor of episodic memory function in ageing (Bender & Raz, 2012; Hertzog, Dixon, Hultsch, & Mac-Donald, 2003). However, where previous studies have predominantly focused on examining the role of WM capacity in age-related episodic memory decline, the current findings provided novel evidence for a relationship between WM and LTM precision in older age. This relationship may arise due to the precision of LTM representations being partly determined by the representational fidelity of this information in WM during encoding, or it may reflect a common mechanism, such as decreased signal-to-noise ratio of neural processing (Li et al., 2001; Welford, 1981), limiting the fidelity of mnemonic representations in both STM and LTM. Interestingly, in the current data we did not observe a significant relationship between WM and LTM precision in the younger group. However, the Bayes factor analyses did not provide strong evidence in favor of this null result, and we did not detect significant age differences in the relationship between WM and LTM precision. Whether a similar relationship between WM and LTM precision is present in younger adults therefore remains to be determined.

Furthermore, we did not observe a significant relationship between perceptual and LTM precision in either of the age groups. However, given the limited power of our small sample size to detect smaller effects (such as $R^2 \sim 0.1$ observed in the current data), as well as lack of substantial evidence in support of the null finding observed in the Bayesian analyses, we cannot exclude a potential contribution of reduced perceptual fidelity in the current age-related deficit in LTM precision. Critically, however, after controlling for individual variability in the precision of both perception and WM, we still observed significant age-related declines in the precision of LTM retrieval. This finding indicates that lower level differences, such as variability in perceptual and WM fidelity, could not fully account for the observed age-related deficit in episodic memory precision. Indeed, this finding suggests additional age-related degradation of information retained in LTM, potentially reflecting accelerated loss of memory fidelity over time in older age, and/or additional noise emerging during retrieval from LTM.

The current findings of differential effects of ageing on the success and precision of episodic memory retrieval imply distinct neurocognitive factors contributing to age-related changes on each component. At the neural level, previous results by Richter et al. (2016) in younger adults have demonstrated the success and precision of episodic memory retrieval to rely on dissociable brain regions of the core recollection network, with retrieval success associated with activity in the hippocampus, and retrieval precision scaling with activity in the angular gyrus. These findings are consistent with the idea that in response to a retrieval cue, the hippocampus initiates memory retrieval via the process of pattern completion (Norman & O'Reilly, 2003), and might provide a threshold memory signal (Norman, 2010; Yonelinas, 2002), denoting instances in which the cue either succeeds or fails to elicit

recollection. Retrieved memories are further reinstated in cortical regions (Bosch, Jehee, Fernández, & Doeller, 2014; Treves & Rolls, 1994; Wheeler, Petersen, & Buckner, 2000), and the angular gyrus may play a role in online representation of the integrated, episodic content (Bonnici, Richter, Yazar, & Simons, 2016; Rugg & King, 2018).

Given the putative roles of the hippocampus and the angular gyrus in the success and precision of episodic memory retrieval, respectively, it might be that the behavioral results observed in the present data map onto distinct age-related functional and structural alterations in these two brain regions. Previous investigations have demonstrated diminished episodic recollection effects in the angular gyrus in older adults (e.g., Daselaar, Fleck, Dobbins, Madden, & Cabeza, 2006; Duarte, Graham, & Henson, 2010), potentially contributing to the impoverished precision of retrieved memories observed here. The absence of age differences in the probability of retrieval success in most task conditions in the current study might seem surprising given previous reports of age-related declines in both function (Daselaar et al., 2006; Dennis et al., 2008) and structure (Raz et al., 2005; Walhovd et al., 2011) of the hippocampus. However, not all studies have observed retrieval-related changes in this region in healthy older adults (Persson, Kalpouzos, Nilsson, Ryberg, & Nyberg, 2011; Wang, Johnson, de Chastelaine, Donley, & Rugg, 2016), with some finding a lack of age effects when controlling for reductions in behavioral performance (de Chastelaine, Mattson, Wang, Donley, & Rugg, 2016), highlighting the importance of distinguishing between functional changes due to age and performance. An interesting question for future studies to address is therefore whether neural changes in these two regions differentially contribute to age-related changes in the success and precision of episodic memory retrieval.

In addition to assessing age-related changes in the success and precision of memory retrieval, we examined whether age-related increases in binding errors may contribute to reductions in episodic memory retrieval in older age in the model comparison analyses outlined in online supplemental materials. Previous research has postulated deficient binding of events and features as a key mechanism of age-related decline in episodic memory (Naveh-Benjamin, 2000; Naveh-Benjamin, Hussain, Guez, & Bar-On, 2003), as well as demonstrated age-related increases in binding errors in WM (e.g., Mitchell, Johnson, Raye, & D'Esposito, 2000; Peich et al., 2013; but see Brockmole, Parra, Della Sala, & Logie, 2008). In the current investigation, we measured binding errors as the probability that participants reported a cued feature of a non-target item from the same study display (e.g., reporting the color of another object from the same study display as the object tested; Bays et al., 2009), but found no evidence for binding errors in the older, or younger, group in any of the LTM tasks or the WM task (see the online supplemental materials for model comparison). It might be that in contrast to previous WM investigations employing simple shape stimuli (e.g., Peich et al., 2013), the object stimuli used in the current experiment resulted in enhanced performance because participants could draw on each object's rich, semantic representation, on which to bind the individual target features. This hypothesis is in line with previous reports demonstrating a benefit of real-word object stimuli for WM performance (Brady, Störmer, & Alvarez, 2016), as well as preserved ability to use semantic information to support memory functioning in older age (Crespo-Garcia, Cantero, & Atienza, 2012; Mohanty, Naveh-Benjamin, &

Ratneshwar, 2016; Naveh-Benjamin, Craik, Guez, & Kreuger, 2005). Alternatively, it is also possible that in the present LTM tasks, participants made binding errors across study displays, potentially driven by semantic or perceptual similarity of the items rather than shared context (i.e., background pictures). Future experiments could distinguish these hypotheses by manipulating the semantic and perceptual relatedness of stimuli both within and across study displays.

The current findings may further have implications for early detection of age-related memory impairments. With the growing ageing population, maintenance of memory abilities in older age is of critical importance from both individual and societal perspectives, emphasizing the need for sensitive behavioral markers of early age-related declines. Previous work suggests that tasks requiring reconstruction of studied stimuli may provide a more sensitive measure of age-related memory decline (Clark et al., 2017), highlighting a potential benefit of continuous report measures, such as those used in the current study. In contrast to more traditional, categorical measures of memory performance, fine-grained multifeatural assessment of retrieval with continuous report measures may prove advantageous for early detection of age-related changes in the complex, multifaceted qualitative aspects of memory retrieval. These types of tasks further have the benefit of disentangling the effects of treatments and interventions on different subcomponents of memory retrieval. Whereas previous work has primarily focused on enhancing the success of memory retrieval, different strategies may be required to ameliorate reductions in retrieval precision, which as indicated by the current data appear to be consistently observed even in healthy older individuals and are often disproportionate to any changes in retrieval success.

In conclusion, the current study used continuous retrieval measures to elucidate the mechanisms of age-related changes in episodic memory, identifying age-related declines in the precision of episodic memory representations. Age-related decreases in the fidelity of episodic memory retrieval were evident even in the absence of age differences in the probability of successful retrieval, suggesting that this aspect of episodic memory might be more sensitive to age-related degradation in the healthy population. Furthermore, age-related declines in mnemonic precision were evident across different object features retrieved from LTM and were influenced, but not fully explained, by age-related reductions in the precision of WM. The findings highlight the benefit of continuous report paradigms for revealing the specific basis of memory impairments associated with older age and call for investigation of potential dissociable neural factors leading to age-related changes in the success and precision of episodic memory retrieval.

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