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Distinguishing the precision of spatial recollection from its success: Evidence from healthy aging and unilateral mesial temporal lobe resection

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ABSTRACT

Successful episodic recollection can vary in the precision of the information recalled. The hypothesis that recollection precision requires functional neuroanatomical contributions distinct from those required for recollection success remains controversial. Some findings in individuals with hippocampal lesions have indicated that precision is dependent on the hippocampus. However, other neuroimaging and lesion studies have implicated regions outside of the mesial temporal lobe (MTL) in precision, such as parietal cortex. To further elucidate distinctions of recollection precision versus success, we examined whether they were differentially sensitive to aging and to unilateral MTL lesions. Precision and success were measured using a novel task that required memory for item-location associations across different spatial contexts. We found impairments in recollection precision, but not success, in older adults (59–80 years) relative to younger adults (18–33 years). Recollection precision was also selectively impaired in individuals with unilateral MTL resections made to treat refractory epilepsy. Moreover, recollection precision was significantly worse when resections included the hippocampus compared to when only non-hippocampal MTL tissue was resected. These findings suggest that the MTL is critically involved in the high-resolution binding required to support spatial recollection precision, and thus provide evidence for functional neuroanatomical differences between recollection success and precision.

1. Introduction

Episodic recollection is the retrieval of an event comprised of arbitrary and complex associations among individual features (Yonelinas, 2002). Recollection has typically been conceptualized as an all-or-none experience, such that individuals can either be successful or unsuccessful at recollecting an event. This is often contrasted with familiarity-based recognition, in which memory for single items can vary in strength without specific recall of event associative information (Eichenbaum et al., 2007; Yonelinas et al., 2010). However, even when recollection is successful, the quality of the information that is retrieved can vary (Berryhill et al., 2007; Harlow and Donaldson, 2013; Harlow and Yonelinas, 2016; Jeye et al., 2016; Parks et al., 2011; Wilding, 2000), with highly precise and detailed memory in some cases (e.g., "the bus stop was on the left side of the street, four blocks ahead of the first stop sign") and more general memory in others (e.g., "the bus stop was on the left side of the street"). Most studies have used paired-associative memory tests, source memory tests, or remember-know paradigms to measure recollection success, but have not objectively assessed varying levels of recollection precision. That is, typical tests of recollection cannot determine if recollection precision is functionally and/or neuroanatomically distinct from general recollection success.

Damage to the hippocampus impairs recollection (Eichenbaum et al., 2007; Giovanello et al., 2003; Konkel et al., 2008; Yonelinas et al., 2002). Numerous studies have also demonstrated that recollection declines with age (Dulas and Duarte, 2012; McIntyre and Craik, 1987; Schacter et al., 1991; Craik and Rose, 2012; Koen and Yonelinas, 2016; Spencer and Raz, 1995). Age-related recollection impairments correspond to reductions in hippocampal integrity (Wolk et al., 2011) and hippocampal-cortical network connectivity (Hampstead et al., 2016; Poppenk and Moscovitch, 2011). However, the tests utilized in these studies predominantly measure recollection success, without corresponding measures of precision.

Experiments involving human MTL lesions have provided some evidence that damage to the hippocampus has a greater impact on recollection precision than success. Kolarik et al. (2016) used a virtual-reality analog of the Morris water maze task (Morris et al., 1982) in which participants were asked to explore a virtual-reality room and were trained to find and later retrieve a target location. A young adult with bilateral hippocampal damage was able to use coarse allocentric

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search strategies to find the target, but demonstrated significant deficits in spatial precision relative to healthy controls (Kolarik et al., 2016). In a similar virtual-reality experiment, five amnestic patients with MTL damage demonstrated precision impairments without deficits of overall recollection success. They spent less time close to the target location relative to age-matched controls, but equal time in the correct general area (Kolarik et al., 2017). In both studies, precision, but not success, was impaired, thereby suggesting a role for the MTL and especially the hippocampus in spatial recollection precision.

However, not all results are consistent with this conclusion. One recent fMRI experiment segregated memory precision from success in younger adults. During recall, recollection success was related to hippocampal activity whereas precision was related to parietal cortex activity (Richter et al., 2016). Furthermore, two patients with bilateral parietal lobe lesions had successful autobiographical memory for general events but showed impairments when probed for specific details (Berryhill et al., 2007). It is therefore possible that precision is supported by regions outside of the MTL, such as the parietal cortex.

Because only few studies using diverse methods have attempted to distinguish the functional neuroanatomy of recollection success from precision, it remains unclear if and how these memory processes are distinct. Furthermore, previous studies have tested spatial recollection within the same visuospatial context in which it was originally encoded. Such tests do not account for the possibility that precision and success could also be supported in part by perceptual recognition processes (Graf and Schacter, 1989; Quamme et al., 2007; Staresina and Davachi, 2010) rather than by relational/associative memory processes. To limit the possible contributions of perceptual memory to success and precision, we tested younger adults, older adults, and adults with unilateral MTL lesions using a memory task in which objects were studied at locations within a background context, and then later tested within a different background context. Importantly, the change in context ensured that recognition of the object-in-scene perceptual information alone could not support accurate performance. Instead, recollection precision and success were necessarily based on the arbitrary link between the object and its associated location. We hypothesized that if recollection precision and success were distinct processes, functional neuroanatomical changes associated with age would differently affect precision versus success in older adults relative to younger adults. Further, we hypothesized that lesions of the MTL, specifically those that included hippocampus, would particularly disrupt precision relative to success.

2. Methods

2.1. Participants

20 younger and 20 older right-handed adults with no history of neurological or psychiatric conditions participated in the experiment. Data from one older adult and one younger adult were excluded for poor memory performance (at least two standard deviations below overall mean performance for each group) and data from one additional younger adult participant was excluded due to computer malfunction. Thus, data from 18 younger adults (mean age = 25.0, range = 18–33 years) and 19 older adults (mean age = 70.57, range = 59–80 years) were included in the final analyses. Adults with unilateral MTL resection, performed as a treatment for refractory epilepsy, also participated (N = 8; mean age = 39.63, range = 22–50 years, described in Table 1). MTL patients participated approximately 3 years after resection surgery (mean = 2.82, SE = 0.26 years). Before surgery, after surgery, and on the day of the experiment, the Wechsler Abbreviated Scale of Intelligence (WASI-II,(Wechsler, 2008)) was administered to characterize verbal comprehension, perceptual reasoning and IQ (Table 1). All participants gave written informed consent and were monetarily compensated for their time, as approved by the Institutional Review Board at Northwestern University.

Table 1
Unilateral MTL resection participant demographics.

					WASI-II		
ID	Age	Hemisphere	Damage	Resection	FSIQ	VCI	PRI
1	31	L	H-	18.1	104	107	106
2	50	L	H-	2.6	99.6	103.6	99.6
3	40	R	H-	23.8	83	85.6	86.6
4	36	L	H-	3.5	108.3	107.3	120.3
5[a]	39	R	H-	38.6	81	82.5	84.5
6[a]	22	L	H+	1.7	118.5	116	118
7	49	R	H+	23.5	90.67	94	84.3
8	50	L	H+	1.3	113.3	108.6	121.3

Each resection participant is characterized based on age, hemisphere of resection (L = Left, R = Right), whether the hippocampus was intact (H+) or removed as part of the MTL resection (H-), and resection volume in milliliters (mL) in standardized space. Mean scores from the Wechsler Abbreviated Scale of Intelligence – Second Edition (WASI-II,(Wechsler, 2008)) including the Full-Scale Intelligence Quotient (FSIQ), Verbal Comprehension Index (VCI), and Perceptual Reasoning Index (PRI).

[a] Participants are missing post-surgery WASI-II assessment.

2.2. Memory paradigm

Participants completed two study-test blocks of an object location memory task adapted from (Bridge and Voss, 2014a, 2014b). During the study phase, participants viewed 24 objects presented at randomized locations on a specific background scene (Yue et al., 2007) on a screen (52.0 × 29.25 cm), viewed with an eye-to-screen distance of ~60 cm. Objects (3.25 × 4.06 cm, (Moreno-Martinez and Montoro, 2012)) were presented one at a time for 3000 ms each. A red dot was centered on top of each object to identify its exact location. Participants were instructed to remember the object locations as accurately as possible. After each study phase, participants played a visuo-spatial distractor task ("Tetris") for 90 s. Following this filled delay, a cued recall test was administered. 24 studied objects were randomly presented one at a time in the center of the screen and participants were required to use a mouse to recall associated locations (for up to 5000 ms) on a different background scene than was presented with the item during study (Fig. 1 A). Distance error (the distance between the location the object was originally studied and the location the object was recalled) was the main dependent variable. The change in background scene between study and test is an important manipulation because it encourages the hippocampal-dependent process of binding independent features (object and location) into an associative event and discourages other strategies involving the perceptual unitization of the object superimposed on the entire scene (Graf and Schacter, 1989; Quamme et al., 2007; Staresina and Davachi, 2010).

Participants completed these study-test blocks as part of a larger experimental design that also included two additional study-test blocks with a "passive" manipulation, where participants were prompted to move each object from the center of the screen to a pre-selected box, and a final recognition test. These data were not analyzed for this report as they did not contribute to our assessment of recollection success versus precision.

2.3. Behavioral analysis

Statistical analyses were done in R (Team, 2013). Trials were scored based on distance error (difference between recalled and studied locations). The threshold for recollection success was determined using two separate approaches. First, we used the geometry of the screen, and defined successful recollection as the trials recalled within the same quadrant as studied. A similar approach has also been used in other spatial memory tests of precision (Kolarik et al., 2017, 2016), as quadrant based success is similar to rodent spatial memory tests (Kesner

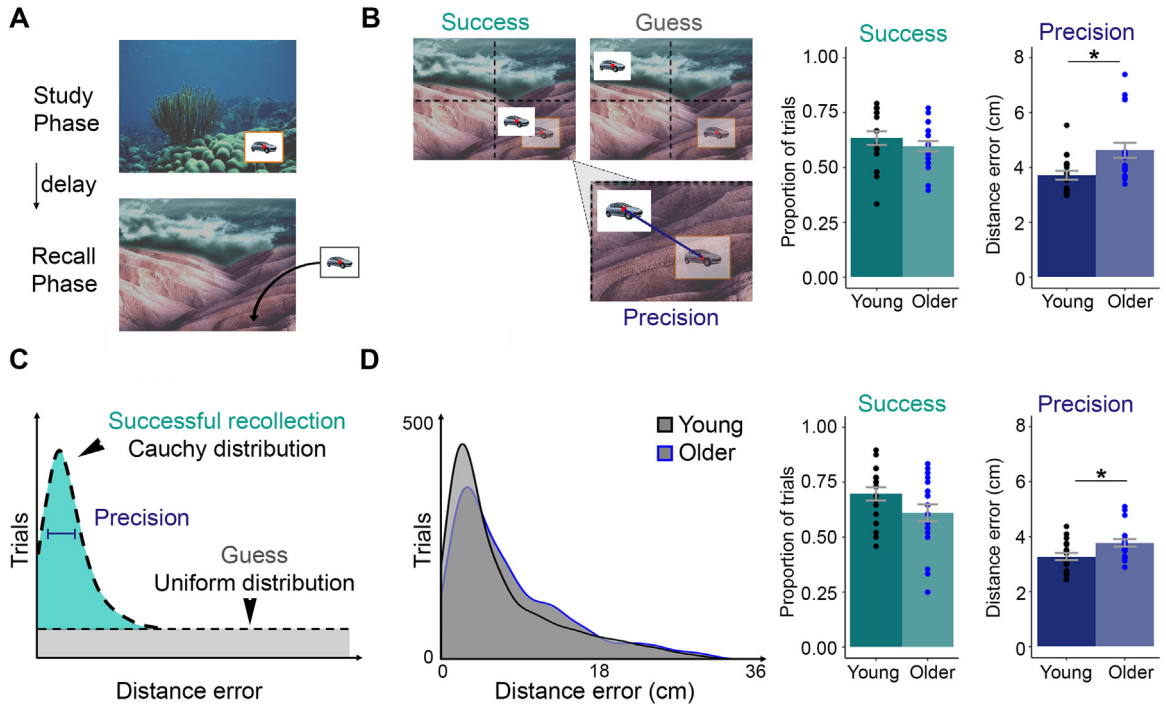

Fig. 1. Recollection precision is impaired in older adults. (A) Participants studied trial-unique objects at randomly assigned locations within a background scene. Subsequent memory testing involved object-cued recall of associated locations on a different background scene. Proportion of trials successfully recollected and mean distance error (recollection precision) of those successfully recollected trials are presented for younger and older adults determined by (B) the geometry of the screen and (C) mixture modeling (see methods). (D) Distributions of distance error are presented for each group. Individual participant scores are marked in blue for older adult participants and black for young adults. Original studied locations are outlined in yellow and quadrant demarcations are for representation in the figure only. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Goodrich-Hunsaker, 2010; Morris et al., 1982). Second, we used growth-mixture modeling (as described in (Harlow and Yonelinas, 2016)) to fit distance error to a Cauchy distribution (for successful recollection) and a uniform distribution (representing random guessing). The modeling results in a mixture parameter (λ) denoting the proportion of success relative to guess. For all participants (excluding those with unilateral temporal lobe resection, N = 37), the mixture-modeling approach indicated that 65.5% of trials fit the Cauchy distributions with a good fit ($p = 0.15$). Distributions for each group demonstrate a slightly sloped guess distribution (rather than uniform flat) due to the relatively low probability that items were either studied or recalled near the corners of the rectangular screen. Although the estimation in mixture modeling is limited by relatively low trial counts (48 trials per participant in this experiment), the fit value that was obtained is consistent with that identified in other studies using similar paradigms (Harlow and Donaldson, 2013; Harlow and Yonelinas, 2016; Nilakantan et al., 2017). Using this modeling approach, the threshold for successful recollection corresponded to 7.66 cm. Recollection precision was then measured as the mean distance error (i.e., the distance between the studied object-location and the recalled location) for trials successfully recollected. Two-sample *t*-tests were used to compare recollection success and recollection precision among groups. For the targeted hippocampal analysis in n = 5 of left hemisphere resection participants, a Welch two-sample *t*-test was used, where variance is not assumed to be equal among groups of small sample sizes.

2.4. Magnetic resonance imaging

To provide anatomical characterization of the unilateral MTL lesions, MRI structural data were collected from these participants using a Siemens 3 T TIM Trio whole-body magnet with a 32-channel head coil. An MPRAGE T_1-weighted scans structural image (TR = 2400 ms, TE = 3.16 ms, FOV = 256 × 256, flip angle = 8°, with 1.0 × 1.0 × 1.0 mm voxel resolution over 176 sagittal volumes) was acquired from each participant. Structural images were preprocessed using AFNI (Cox, 1996). Each structural image was AC-PC aligned and transformed to Talaraich-Tournoux (stereotaxic) space. Each resection was then manually drawn as a mask using the contralateral hemisphere as reference. Whole brain-volume was estimated using a manually inspected AFNI brain segmentation from the structural scan, plus the estimated volume of resected tissue.

3. Results

3.1. Is recollection precision and/or success affected by healthy aging?

Overall memory performance (mean distance error for all trials, irrespective of any success or precision distinction) was not significantly different for younger (mean = 6.83, SE = 0.50 cm) compared to older adults (mean = 7.94, SE = 0.54 cm) ($T(35) = 1.50$, $p = 0.14$).

We first used the geometry of the screen to characterize recollection success and precision (Fig. 1B). Recollection success was not significantly different for younger adults (mean = 63.43%, SE = 3.13%) compared to older adults (mean = 59.64%, SE = 2.39%) ($T(35) = 0.96$, $p = 0.34$). However, recollection precision was impaired for older adults (mean = 4.63, SE = 0.27 cm) relative to younger adults (mean = 3.72, SE = 0.16 cm) ($T(35) = 2.82$, $p = 0.008$).

Results were consistent when we used a mixture-modeling approach to define recollection success versus precision (Fig. 1C). Recollection success did not significantly differ for younger adults (mean = 69.7%, SE = 2.99%) compared to older adults (mean = 61.1%, SE = 3.84%) ($T(35) = 1.75$, $p = 0.09$). However, recollection precision was impaired for older adults (mean = 3.78 cm, SE = 0.14 cm) relative to younger adults (mean = 3.28 cm, SE = 0.13 cm; $T(35) = 2.65$, $p = 0.01$, Fig. 1D).

To further establish the specificity of these age-related effects on

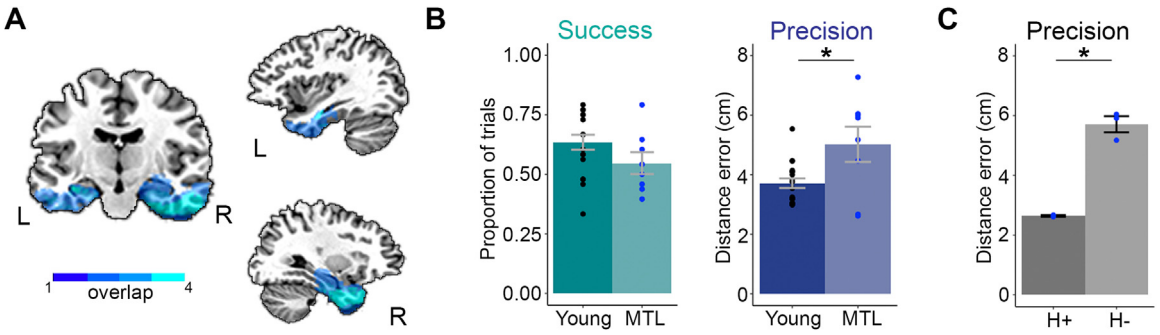

Fig. 2. Recollection precision is impaired in individuals with unilateral mesial temporal lobe (MTL) resection. (A) Overlap map depicting resected MTL tissue (with brighter colors representing more overlap across participants). (B) Mean recollection success and recollection precision of individuals with unilateral MTL resection relative to younger adults. (C). Recollection precision for left hemisphere resection participants whose hippocampus was removed (H-) as part of the MTL resection relative to participants whose hippocampus remains intact (H+). Individual participant scores are marked in blue for MTL resection participants and in black for young adults. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

precision, we tested the effects of aging on distance error for guess trials. Recollection precision for younger adults (mean = 14.64 SE = 0.45 cm) was not significantly different compared to older adults (mean = 14.35 cm, SE = 0.36 cm) ($T(35) = 0.51$, $p = 0.61$). Therefore, we found that age selectively impaired recollection precision, but not recollection success or guess distance errors.

3.2. Is MTL necessary for recollection precision and/or success?

To test the role of the MTL in recollection success and precision, we assessed memory performance in individuals with unilateral MTL resections. The amount of tissue resected varied among these participants, with most resections limited to the anterior third of the MTL (Table 1, Fig. 2A). Overall memory performance (mean distance error) was marginally worse for individuals with MTL resection (mean = 9.06 cm, SE = 1.14 cm) relative to younger adults (mean = 6.83 cm, SE = 0.50 cm; $T(24) = 2.1$, $p = 0.045$). To use the modeling approach to dissociate recollection precision from success, the distribution of distance error must reliably fit the canonical Cauchy-uniform distribution (described in Fig. 1C). However, the distribution of distance error for individuals with MTL resections were highly variable and as a group, they did not demonstrate a consistent mixed cauchy-uniform distribution of distance error. Recollection success was therefore only defined using the quadrant approach, as in other studies involving individuals with MTL lesions (Kolarik et al., 2017, 2016). Recollection success was not significantly different for individuals with unilateral MTL resection (mean = 54.69%, SE = 3.13%) than for the younger adults ($T(24) = 1.56$, $p = 0.13$). Recollection precision was significantly impaired for individuals with unilateral MTL resection participants (mean = 5.02 cm, SE = 0.59 cm) relative to the younger adults (mean = 3.72 cm, SE = 0.16 cm; $T(24) = 2.87$, $p = 0.008$; Fig. 2B). Notably, although participants with unilateral MTL resections were older than younger adult controls ($T(24) = 5.14$, $p < 0.001$), there was a wide range of ages for MTL resection participants. Furthermore, there was no significant correlation between age and recollection precision for the MTL resection participants ($r = 0.139$, $p = 0.74$; Table 1), suggesting that age did not contribute significantly to the precision impairments attributed to MTL lesions.

We next tested whether MTL lesions that included the hippocampus were especially disruptive for precision rather than success, compared to MTL lesions that did not include the hippocampus. The right-hemisphere resection patients overall had greater amount of tissue removed and lower IQ than left-hemisphere resection patients, and so we restricted this analysis to left-lateralized (n = 5) resection patients (Fig. 2C). Individuals whose left MTL resections included the hippocampus (H-, n = 3, mean = 5.71, SE = 0.27 cm) had worse precision relative to those resections which did not include the hippocampus (H+, n = 2, mean = 2.64, SE = 0.03 cm) ($T(2.04) = 11.27$, $p = 0.007$). However, recollection success did not vary significantly for H- versus H+ participants (H-: mean = 45.83%, SE = 4.33%; H+: mean = 71.8%, SE = 7.73%) ($T(1.72) = 3.07$, $p = 0.11$). The amount of tissue resected did not differ for the two groups (H- mean = 8.06 SE = 5.03 mL; H+ mean = 1.53 SE = 0.19 mL) ($T(2.01) = 1.30$, $p = 0.32$), even when corrected for estimated whole-brain volume (H- mean = 0.50, SE = 0.31%; H+ mean = 0.09 SE = 0.38%; $T(2.00) = 1.32$, $p = 0.32$).

4. Discussion

We examined recollection precision and success in younger adults, older adults, and individuals with unilateral MTL resections. Our task probed the associative/relational components of precision and success by assessing object-location memory in different background contexts than were studied. The change in background scene prevents perceptual recognition strategies involving encoding the object and background scene as a single unit (Graf and Schacter, 1989; Quamme et al., 2007; Staresina and Davachi, 2010). Older adults showed a specific impairment for recollection precision but not success, and no overall memory impairment, relative to younger adults. Precision impairment in older adults could be related to altered MTL function and structure, as many memory impairments due to age are associated with atrophy of the hippocampus, diminished structural connectivity, and altered functional connectivity of the MTL (Andrews-Hanna et al., 2007; Bakkour et al., 2013; Leal and Yassa, 2013; Pini et al., 2016), although such functional neuroanatomical changes were not measured in the present study. The necessary contribution of the MTL was assessed with individuals with unilateral surgical resections of MTL tissue. While overall performance was impaired relative to controls, precision was significantly impaired with no impairment of success. Notably, resections that included hippocampal tissue produced significantly worse precision compared to resections that included only non-hippocampal MTL tissue, with no significant difference in success. Thus, recollection success and precision were distinguished by the functional neuroanatomical changes of healthy aging as well as by MTL lesions, particularly those involving the hippocampus.

Our results are consistent with other studies of spatial episodic memory that did not limit the role of perceptual memory in success and precision. In those studies, MTL and hippocampal damage was related to impairments in recollection precision rather than in general spatial strategy or recollection success (Kolarik et al., 2017, 2016). There are notable caveats to our findings as well as to these previous studies. Although the change in background scene was designed to prevent perceptual recognition strategies, it could have also increased interference from the new scene background on recall performance, which could affect different memory processes (Sun et al., 2017) and have

harmed MTL-resection and older adult participants more so than younger adult participants (Fidalgo et al., 2016; Watson and Lee, 2013). Furthermore, our analysis was limited by our small sample size, which included only two individuals with resections that spared the hippocampus. Evidence demonstrating a role for the hippocampus in recollection precision would be strongest in a larger cohort with comparisons to a control group with brain lesions outside of the MTL. Precision impairments due to hippocampal damage do not rule out the possibility that other regions, such as parietal cortex, make critical contributions to precision. Indeed, there is lesion (Berryhill et al., 2007) and fMRI (Richter et al., 2016) evidence for parietal cortex involvement in recollection precision, with the fMRI data indicating that parietal cortex might be particularly involved during memory retrieval (Richter et al., 2016). Future studies could include additional perceptual controls, compare the effects of MTL lesions to parietal lesions on memory success versus precision, and fMRI studies in particular could determine whether these regions are differentially involved during memory formation versus retrieval.

It is important to note that tissue damage can impact large-scale network function (Gratton et al., 2012), including lesions of the hippocampus (Henson et al., 2016; Voets et al., 2014). Likewise, although aging disproportionately impacts MTL-network function (Jagust, 2013), normal aging can involve a variety of neurological changes, including abnormal protein aggregation and distributed neurodegeneration (Jack et al., 2013). It is therefore possible that memory precision and success are supported by different patterns of hippocampal-cortical connectivity. Support for this hypothesis comes from our previous studies in which a repetitive TMS protocol that increases functional connectivity among the hippocampus and regions of the posterior-medial parietal and occipital cortex (Wang et al., 2014) resulted in a selective increase in recollection precision without affecting success (Nilakantan et al., 2017). Nonetheless, the current results that hippocampal damage was particularly detrimental for precision relative to other non-hippocampal MTL tissue suggests that the hippocampus is critical for high-resolution memory (Yonelinas, 2013).

The present results are also consistent with studies of visual working memory (Zhang and Luck, 2008), which demonstrate impaired high-resolution but not low-resolution memories or general memory capacity in aging (Peich et al., 2013; Pertzov et al., 2015) and in individuals with bilateral hippocampal damage (Koen et al., 2017; Watson et al., 2013). One short-term memory study demonstrated seemingly contradictory results, suggesting that the hippocampus is not necessarily involved in memory precision (Warren et al., 2014). In this study, participants studied boxes shown in specific associated colors, and trials included one, three, or six boxes at a time. After a brief delay, cued with a box's location, participants had to select the associated color using a continuous color wheel scale. A modeling approach was then used to segregate the probability that the item was remembered relative to the quality (color precision) of the item. Amnestic patients were less likely to remember items at test overall, but showed no impairment for the quality of the associated color (Warren et al., 2014) for all trials. However, when load was matched to the other studies of precision (only one item-color association was studied at a time), four of the five amnesic patients showed no impairment of general recollection yet demonstrated reduced recollection precision relative to controls. Thus, the lack of relative precision impairment only emerged with greater loads, suggesting that precision is impaired in both amnesics and controls when high-resolution information about multiple items must be maintained (see also Jeneson et al., 2010, 2012). Although the current results are agnostic to whether short versus long retention intervals are required to observe recollection precision impairments following MTL damage, they further support the conclusion that the hippocampus is necessary to bind complex and high-resolution information (Yonelinas, 2013), and that this remains the case even when perceptual qualities of the stimulus alone could not govern precision performance.

It is also important to note that recollection is usually tested using tasks that do not explicitly measure precision versus success, and such recollection tasks are consistently impaired by hippocampal damage (Aggleton et al., 2005; Scoville and Milner, 1957). This raises the question of why performance is affected in such tasks if hippocampal impairments are relatively specific to precision. It is possible that many of these tests involve recollection of varying degrees of qualitative information, and that precision is therefore relevant to performance even though it is not specifically measured. Furthermore, although recollection precision and success are orthogonal in theory (Bays et al., 2009) and could therefore potentially be dissociated, recollection precision depends on success in our experiment and in others that have attempted to distinguish them. That is, memory for high-resolution details are not assessed (i.e., “the bus stop is four blocks ahead of the first stop sign”) without successful recollection (i.e., “the bus stop was on the left”). Experiments that systematically address these questions are necessary to fully understand neural mechanisms for memory precision and how they might relate to those of other memory processes. Nonetheless, our results provide evidence that memory precision and success are supported by distinct functional neuroanatomy, with the MTL and the hippocampus particularly involved in recollection precision.

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Declarations of interest

None.

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