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Intrinsic functional connectivity in medial temporal lobe networks is associated with susceptibility to misinformation

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ABSTRACT

Memory is notoriously fallible and susceptible to misinformation. Yet little is known about the underlying cognitive and neural mechanisms that render individuals vulnerable to this type of false memory. The current experiments take an individual differences approach to examine whether susceptibility to misinformation reflects stable underlying factors related to memory retrieval. In Study 1, we report for the first time the existence of substantial individual variability in susceptibility to misinformation in the context of repeated memory retrieval, when the misinformation effect is most pronounced. This variability was not related to an individual's tendency to adopt an episodic retrieval style during remembering (trait mnemonics). In Study 2, we next examined whether susceptibility to misinformation is related to intrinsic functional connectivity in medial temporal lobe (MTL) networks known to coordinate memory reactivation during event retrieval. Stronger resting-state functional connectivity between the MTL and cortical areas associated with visual memory reactivation (occipital cortex) was associated with better protection from misinformation. Together, these results reveal that while memory distortion is a universal property of our reconstructive memory system, susceptibility to misinformation varies at the individual level and may depend on one's ability to reactivate visual details during memory retrieval.

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Misinformation; functional connectivity; memory reactivation; resting-state

Introduction

When exposed to misleading information about a past event, individuals frequently incorporate misleading details into memory, resulting in memory errors in which misleading details are later remembered as part of an original event (Loftus, 2005). This robust memory distortion, coined the misinformation effect, becomes magnified when individuals recall event details before exposure to misinformation (i.e., "retrieval enhanced suggestibility"), a situation that is common in everyday memory recall as well as eyewitness remembering (Chan et al., 2009; Thomas et al., 2010). An important outstanding question is what underlying cognitive and neural mechanisms render individuals susceptible to this type of false memory.

Prior research suggests that false memory due to misinformation reflects faulty reconstructive processes during memory retrieval and aberrant memory reactivation. Memory reactivation is a central tenent of episodic memory retrieval involving re-expression of neural activity evoked in sensory cortex during initial perceptual experience (Favila et al., 2020). The medial temporal lobe (MTL) is thought to orchestrate cortical reactivation to enable detailed reexperiencing of past events (Staresina et al., 2012). In the context of the misinformation effect, the misattribution of events to misleading rather than accurate sources of information has been linked to reduced reactivation of brain regions involved in the initial encoding of event details and increased reactivation of brain regions involved in the encoding of misleading details during memory retrieval (Karanian et al., 2020; Stark et al., 2010). For example, in a study by Stark and colleagues (2010), participants encoded original event details in the visual modality and then were exposed to misleading post-event information in the auditory modality. During a later test of memory, accurate memory for the original event was associated with greater activity in the MTL and visual processing regions (occipital cortex), whereas false memory due to misinformation was associated with reduced occipital activity and increased activity in auditory processing regions (auditory cortex).

Additional evidence that MTL-mediated cortical reactivation underlies memory accuracy in the face of misinformation comes from a recent study by Karanian and colleagues (2020). Similar to the study by Stark and colleagues (2010), participants encoded visual event details and then were exposed to misleading details in an

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auditory narrative before being given a final memory test. Participants were also given an initial test of memory prior to exposure to misinformation to potentiate the misinformation effect. Importantly, some participants received a warning about the reliability of the auditory narrative before or after exposure to misinformation. At the behavioural level, participants who received a warning demonstrated less susceptibility to misinformation on the final memory test compared to unwarned participants. At the neural level, participants who received a warning demonstrated increased activity in visual regions associated with the original source of information as well as decreased activity in auditory regions associated with the misleading source of information. Importantly, stronger visual cortex reactivation was associated with reduced susceptibility to misinformation, whereas stronger auditory cortex reactivation was associated with increased susceptibility to misinformation. In both cases, sensory-specific reactivation during memory retrieval was related to activity in the MTL. Together, these results provide additional evidence that memory accuracy in the face of misinformation reflects MTL-mediated reactivation of sensory-specific cortices during memory retrieval, and that protection from misinformation involves the reactivation of cortical regions (e.g., visual cortex) associated with original events.

The current study builds upon this prior work to investigate whether susceptibility to misinformation also reflects individual differences in memory retrieval and the neural circuits underlying memory retrieval. It is well established that individuals vary substantially in how well they remember the past and the degree to which their memories contain specific details versus the schematic gist of past episodes (Bors & MacLeod, 1996). Importantly, much of the variance in performance across tests of episodic memory can be explained by individual differences in the strength of MTL activity and MTL-mediated cortical reactivation (Trelle et al., 2020). Intrinsic MTL-cortical connectivity at rest also relates to more stable trait-like differences in how individuals recall the past. For example, Sheldon and colleagues (2016) used the Survey of Autobiographical Memory (SAM; Palombo et al., 2013) to measure individual differences in memory retrieval style, identifying whether individuals tend to recover rich sensory and contextual details from prior events in everyday life (episodic retrieval style) or tend to recover more general semantic knowledge devoid of event details (semantic retrieval style). They also measured intrinsic connectivity patterns of the MTL memory system at rest. When comparing the neural and behavioural measures, Sheldon and colleagues found that functional connectivity between parahippocampal gyrus and posterior brain regions involved in visual processing (e.g., occipital cortex) was positively related to both episodic retrieval style and a bias to recover detailed episodic information over semantic information during memory retrieval (calculated as episodic – semantic SAM scores). These results suggest that intrinsic individual variability in MTL network connectivity, and MTL connectivity to brain regions that support visual reactivation in particular, plays an important role in naturalistic memory performance.

To date, few studies have investigated whether similar individual difference factors also underlie *mis*remembering and susceptibility to misinformation. As is the case for true memory, individuals vary in their degree of false memory (Dewhurst et al., 2018; Salthouse & Siedlecki, 2007; Unsworth et al., 2009; Unsworth & Brewer, 2010). However, prior research has suggested that while some cognitive factors may be associated with individual differences in false memory, there is no false memory "trait" and memory distortion due to misinformation is ubiquitous across individuals (Nichols & Loftus, 2019; Patihis, 2018; Zhu et al., 2010). Indeed, even individuals with highly superior autobiographical memory demonstrate a robust misinformation effect (Patihis et al., 2013). Nevertheless, variability across individuals has been observed in prior studies of the misinformation effect, and it has been argued that susceptibility to misinformation itself can act as an individual difference variable (Calvillo, 2014; Loftus et al., 1992; Tomes & Katz, 1997). For example, Tomes and Katz (1997) found that some individuals demonstrate a consistent or "habitual" tendency to be susceptible to misinformation, even when misinformation is presented on separate occasions to different events, whereas others do not demonstrate such a tendency.

Here, we investigate whether individual variability in susceptibility to misinformation relates to factors underlying accurate versus inaccurate memory retrieval and an individual's propensity to recover vivid sensory-specific details during remembering. In Study 1, we investigate this relationship at the behavioural level, with two primary goals. First, we aimed to investigate whether substantial individual variability is present with respect to memory performance in a repeated retrieval misinformation paradigm. As described previously, if participants are asked to remember details of an event immediately after witnessing it, they are more likely to incorporate misleading information about those events into memory than if they did not receive an immediate test of memory (Chan et al., 2009; Thomas et al., 2010). An outstanding question is whether substantial individual variability in susceptibility to misinformation is present in this repeated retrieval context. To investigate this question, participants in Study 1 completed a misinformation memory paradigm (see Karanian et al., 2020) in which they watched a video of a crime, took an immediate test of memory, listened to an audio narrative recounting the original crime event that contained misinformation, and then took a final test of memory. The distribution of memory accuracy scores on misleading trials was used as a measure of individual variability in susceptibility to misinformation.

A second goal of Study 1 was to investigate the degree to which variability in susceptibility to misinformation relates to an individual's natural tendency to retrieve detailed episodes versus more general semantic knowledge during remembering. To examine this possibility, all participants who completed the misinformation memory paradigm also completed the Survey of Autobiographical Memory (SAM), and the relationship between factor scores for trait mnemonics (episodic and semantic memory) and memory accuracy on misleading trials was tested. If susceptibility to misinformation reflects a tendency to recover more general semantic knowledge versus vivid sensory details of an original event, we predicted that a significant relationship between SAM scores and susceptibility to misinformation would be observed. Specifically, better memory accuracy on misleading trials should be positively associated with episodic SAM scores and episodic bias scores, and negatively associated with semantic SAM scores.

In Study 2, we next used fMRI to investigate whether individual variability in susceptibility to misinformation has a neural basis and relates to intrinsic functional connectivity in MTL networks associated with sensory reactivation during memory retrieval. A subset of participants who participated in the prior misinformation study by Karanian and colleagues (2020) also completed a resting-state scan. Resting-state functional connectivity (rsFC) in MTL networks was measured using two different MTL seed regions (bilateral parahippocampal gyrus and hippocampus) and susceptibility to misinformation (memory accuracy on misleading trials) was related to the strength of MTL connectivity to cortical regions. If variability in susceptibility to misinformation reflects individual differences in the reinstatement of past events and reactivation of visual processing areas associated with those events, then memory accuracy on misleading trials should be related to intrinsic MTL connectivity with posterior brain regions that support the reactivation of visual details (e.g., occipital cortex).

Study 1: behavioural study

Methods

Participants

A total of 81 adults aged 18–35 participated in the experiment through the online platform *Prolific*. All participants were native English speakers, had normal or corrected-to-normal vision, and reported no history of traumatic head injury. Sample size was determined using G*Power (Faul et al., 2007) to ensure sufficient power to detect a significant correlation between susceptibility to misinformation and trait mnemonics (as measured by the SAM). It was determined that a total sample size of 67 participants would be required in order to obtain a power level of $1 - \beta = 0.80$ (alpha level of .05, effect size of .3). However, given that this experiment was run virtually and some attrition was expected, data from 81 participants was collected. The study was approved by the Institutional Review Board at Tufts University (#1844011) and all participants provided written informed consent. Five participants were excluded due to failing attention checks or for not finishing the experiment and three participants were excluded due to poor test performance (memory accuracy less than two standard deviations from group mean), for a final sample of $n = 73$.

Procedure

Misinformation paradigm

Participants completed a misinformation protocol adapted from Karanian and colleagues (2020). The misinformation protocol involved four primary phases: (1) Video of witnessed event, (2) Initial memory test, (3) Audio narrative, (4) Final memory test (Figure 1).

Video of witnessed event. Participants first viewed a 22-min video clip from the black and white silent film Rififi. The video depicts the events surrounding a burglary of a jewellery store and contains no dialogue.

Initial memory test. Immediately following the video, participants were administered the initial memory test, which consisted of 24 questions which appeared on a computer monitor one at a time and asked about a critical detail from the witnessed event. All questions were probed in chronological order (e.g., the same order that they appeared in the video). Four alternative answers were displayed below each question and consisted of the correct detail shown in the video, a misleading detail, and two highly plausible lures (as determined by pilot testing). The order of the four alternative answers was randomised across tests and participants. For each question, participants indicated their response with a button press on a computer keyboard. Participants then indicated their confidence in their response by entering a numerical rating on a sliding scale from 0 (guess) to 100 (very confident) on the computer keyboard. All questions and confidence ratings were self-paced and participants could not return to a question once they had indicated their answer. After the initial memory test, participants were given an attention check question and then played the game “2048” as a filler task for ten minutes. Following the filler task, participants were given one additional attention check question. The following is an example of an attention check question: “ … When asked for your favorite color you must enter the word ‘green’ in the text box below. Based on the text you read above, what color have you been asked to enter?”.

Audio narrative. Participants next listened to a narrative synopsis of the witnessed event which consisted of 115 sentences, 24 of which contained critical details that would be probed during the memory test. Critical sentences either (1) accurately described a detail (underlined) from the original event (consistent) (e.g., “Revealed at the bottom of the case is a rope.”), (2) inaccurately described a detail from the original event (misleading) (e.g., “Revealed

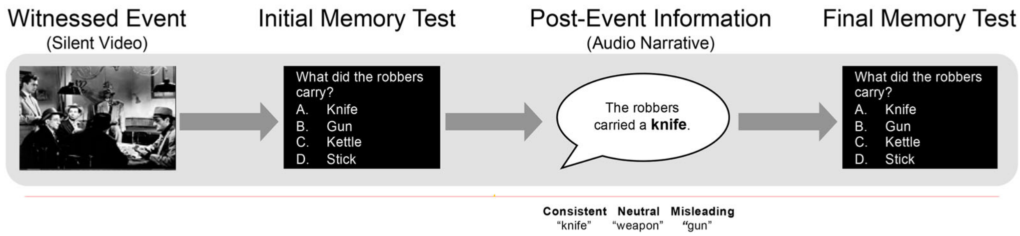

Figure 1. Eyewitness memory paradigm used in Study 1 and Study 2. Participants watched a silent video depicting a crime (witnessed event) and were then given an immediate test of recognition memory (initial memory test). Participants then listened to an audio narrative in which they were provided with post-event information that contained critical details that were either consistent, neutral, or misleading with respect to the original event. After the audio narrative, participants were given a final recognition memory test probing their memory for the original witnessed event.

at the bottom of the case is a towel."), or (3) provided an alternative (neither consistent nor inconsistent) detail from the original event (neutral) (e.g., "Revealed at the bottom of the case is a useful object."). An equal number of critical sentences contained consistent, misleading, or neutral details. Each critical detail appeared only once during the narrative and the assignment of each detail to the consistent, neutral, or misleading condition was counterbalanced across participants. All filler sentences were consistent with the content of the video such that the majority of the sentences in the audio narrative described accurate information. Filler sentences were not probed in the memory tests.

Final memory test. Immediately following the audio narrative, participants were administered the final memory test, which probed their memory for the critical details from the original witnessed event (video) in the same manner as the initial memory test.

Survey of Autobiographical Memory (SAM)

Following the final memory test, participants filled out a demographic questionnaire and the short version of the Survey of Autobiographical Memory (SAM; Palombo et al., 2013). The SAM is a self-report assessment of mnemonic traits in which participants rate the degree to which a statement describes their memory ability using a 5-point Likert scale. Statements assess autobiographical episodic memory (eight items; e.g., "When I remember events, in general I can recall people, what they looked like, or what they were wearing"), semantic memory (six items; e.g., "I can learn and repeat facts easily, even if I don't remember where I learned them"), spatial memory (six items; e.g., "After I have visited an area, it is easy for me to find my way around the second time I visit"), and future thinking (six items; e.g., "When I imagine an event in the future, the event generates vivid mental images that are specific to time and place"). Weighted sums of the statements produce factor scores for each subscale (episodic, semantic, spatial, future thinking). The current study focused on episodic and semantic factor scores to measure trait episodic and semantic remembering. The episodic memory subscale captures one's ability to subjectively remember specific contextual details about past events whereas the semantic subscale captures one's ability to recall facts or knowledge (Palombo et al., 2013; Sheldon et al., 2016). We also computed an episodic – semantic difference score as a measure of episodic bias in trait mnemonics that controls for overall declarative memory ability.

Data analysis

Memory test and susceptibility to misinformation. Data analysis focused on recognition memory performance (proportion correct) on the final memory test, which was calculated by dividing the number of test trials in which participants selected the correct video detail within each trial type (consistent, neutral, misleading) by the total number of trials for that given trial type (consistent, neutral, misleading). Susceptibility to misinformation was defined as memory accuracy on misleading trials. To test whether memory accuracy differed across trial types, memory accuracy for each trial type was first entered into ANOVA. Follow-up pairwise comparisons were then performed to directly compare memory accuracy on misleading trials to the other trial types (consistent, neutral).

Relationship to trait mnemonics. To investigate the relationship between susceptibility to misinformation and trait mnemonics, Pearson correlations were performed between memory accuracy on misleading trials and the episodic and semantic factor scores of the SAM as well as the episodic bias score (episodic SAM – semantic SAM). We hypothesised that accuracy on misleading trials would be positively associated with episodic trait scores as well as episodic bias scores and negatively related to semantic trait scores. Bayes Factors (BF) were also computed for all null effects related to our hypotheses of interest.

Results

Memory test and susceptibility to misinformation. Accuracy on the initial memory test was similar to what has been observed in previous repeated testing paradigms ($M = .67$; Chan et al., 2009; Karanian et al., 2020). Of primary interest was memory accuracy during the final memory test. As shown in Figure 2(A), recognition memory for original event details differed according to how the details had been described in the post-event

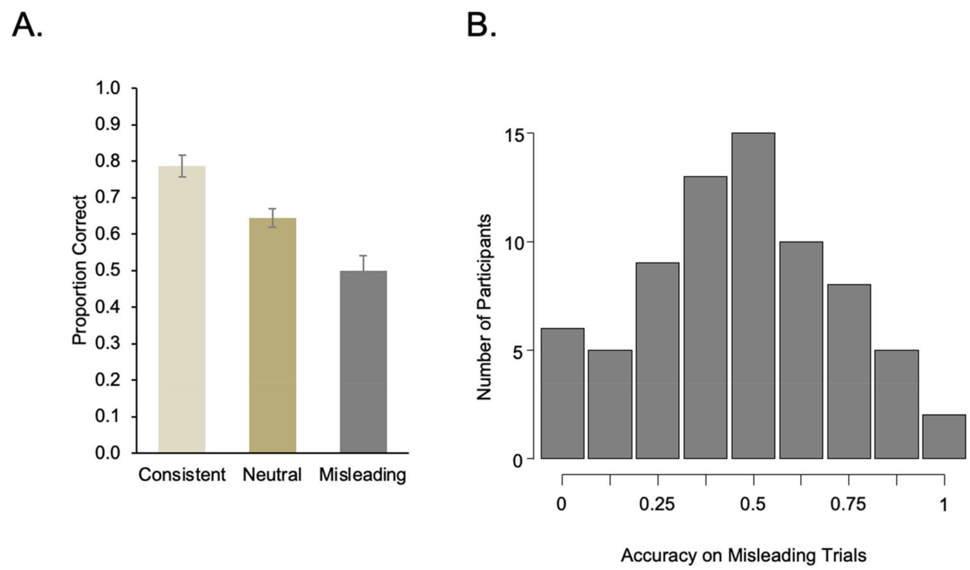

Figure 2. Behavioural results from Study 1. (A) Results from the final memory test. Memory accuracy (proportion correct) within each trial type (consistent, neutral, misleading). Error bars indicate SEM. (B) Individual variability in susceptibility to misinformation (memory accuracy on misleading trials).

narrative (consistent, neutral, control; $F(2, 144) = 56.42$, $p < 0.001$, $\eta_p^2 = 0.44$). Importantly, a strong misinformation effect was observed whereby memory performance was significantly reduced on misleading trials compared to both neutral trials (t $(72) = 5.69$, $p < 0.001$, $d = 0.67$, 95% CI [0.41, .92]) and consistent trials (t $(72) = 9.39$, $p < 0.001$, $d = 1.10$, 95% CI [.81, 1.39]). Memory accuracy was also reduced for neutral trials (when original event details were described generally in the post-event narrative) compared to consistent trials (when original event details were described accurately in the post-event narrative) (t $(72) = 5.79$, $p < 0.001$, $d = 0.68$, 95% CI [.42, .93]), consistent with what has been previously observed in the literature (e.g., Karanian et al., 2020).

Susceptibility to misinformation (memory accuracy on misleading trials) varied sizably across individuals, ranging from a magnitude of 0–1 (Figure 2(B)). Post-hoc analysis indicated that this between-subjects variability in susceptibility to misinformation was not related to general memory performance (accuracy on consistent trials; $r(71) = .12$, $p = .36$, $BF_{10} = .22$), indicating that variability in susceptibility to misinformation is unlikely to simply reflect individual differences in overall memory ability.

SAM. SAM episodic and semantic factor scores are plotted in Figure 3(A) and episodic bias scores (episodic SAM – semantic SAM) are plotted in Figure 3(B). Substantial individual variability in autobiographical retrieval style was evident in the distribution of the episodic bias scores, with approximately half of the sample displaying a greater tendency to engage in episodic than semantic remembering (positive values; $n = 31$) and approximately half of the sample displaying a greater tendency to engage in semantic than episodic remembering (negative values; $n = 42$).

Relationship between susceptibility to misinformation and trait mnemonics. We next investigated whether susceptibility to misinformation (memory accuracy on misleading trials) was related to individual differences in trait mnemonics. Susceptibility to misinformation was not related to participants' episodic factor score ($r(71) = -.02$, $p = .84$, $BF_{10} = .15$; Figure 4(A)) nor participants' semantic factor scores ($r(71) = -.06$, $p = .63$, $BF_{10} = .16$; Figure 4(B)). In addition, there was not a significant association between susceptibility to misinformation and episodic bias scores ($r(71) = .04$, $p = .75$, $BF_{10} = .15$; Figure 4(C)). Post-hoc analysis directly compared the group of participants who endorsed a greater episodic retrieval tyle (episodic bias) to those who endorsed a greater semantic retrieval style (semantic bias). Mirroring the correlation results, susceptibility to misinformation did not differ between the two groups (t $(71) = .24$, $p = 0.81$, $d = 0.06$, 95% CI [−.52, .41], $BF_{10} = .25$).

Interim discussion

Study 1 investigated susceptibility to misinformation in the context of a repeated memory retrieval paradigm, when individuals retrieve information about an original event before being exposed to misinformation, mirroring real-world eyewitness contexts. Prior research has shown that memory errors due to misinformation are more frequent in such repeated retrieval contexts. Here, we demonstrate that while a strong misinformation effect occurs in the context of repeated memory retrieval, individuals vary substantially in the extent to which they make memory errors in this context, with some individuals showing complete immunity from misinformation. Of primary interest was whether this individual variability in susceptibility to misinformation is related to memory

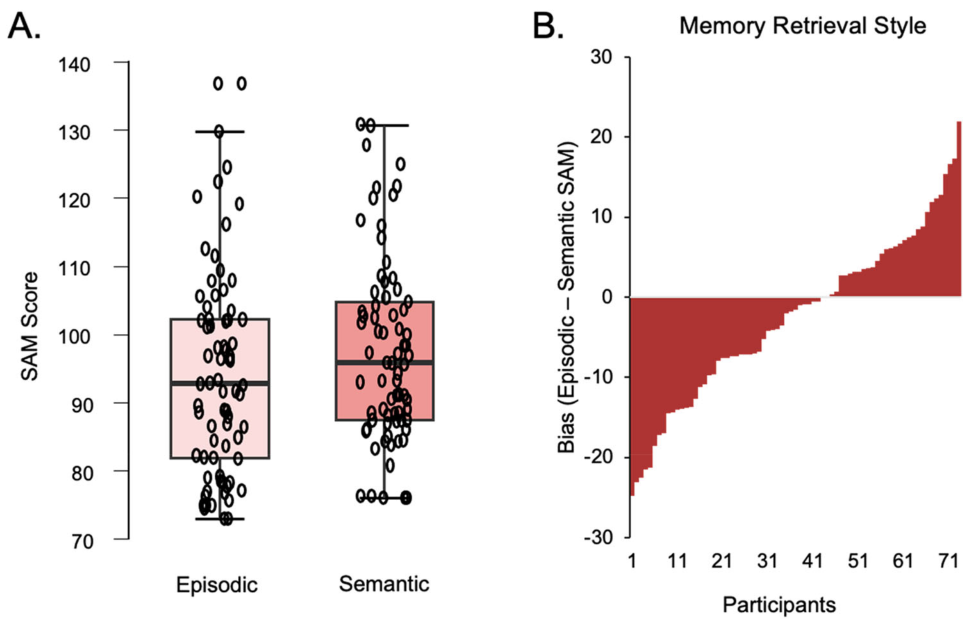

Figure 3. Data from the Survey of Autobiographical Memory (SAM). (A) Factor scores for the episodic SAM (left) and semantic SAM (right). (B) Individual variability in trait mnemonics represented as an episodic bias scores (episodic SAM – semantic SAM). Positive bias scores indicate a retrieval style biased towards detailed episodic information (episodic retrieval style). Negative bias scores indicate a retrieval style biased towards more general semantic knowledge (semantic retrieval style).

retrieval style, or the degree to which an individual tends to rely on more specific episodic details versus more general semantic knowledge during memory retrieval (trait mnemonics). Although substantial individual variability in memory retrieval style was present in our sample, we did not observe a relationship between memory accuracy on misleading trials and trait mnemonics. Misinformation susceptibility was not related to episodic or semantic SAM factor scores nor was it related to individuals' episodic bias in memory retrieval (episodic – semantic scores). In Study 2, we turn to fMRI to investigate the underlying neural mechanisms that might contribute to individual variability in susceptibility to misinformation. Specifically, we tested whether susceptibility to misinformation relates to intrinsic functional connectivity in MTL networks associated with memory reactivation.

Study 2: fMRI study

Methods

Participants

A total of 47 adults aged 18–35 participated in the experiment. All participants were native English speakers, right-handed, had normal or corrected-to-normal vision, and reported no history of traumatic head injury. Participants

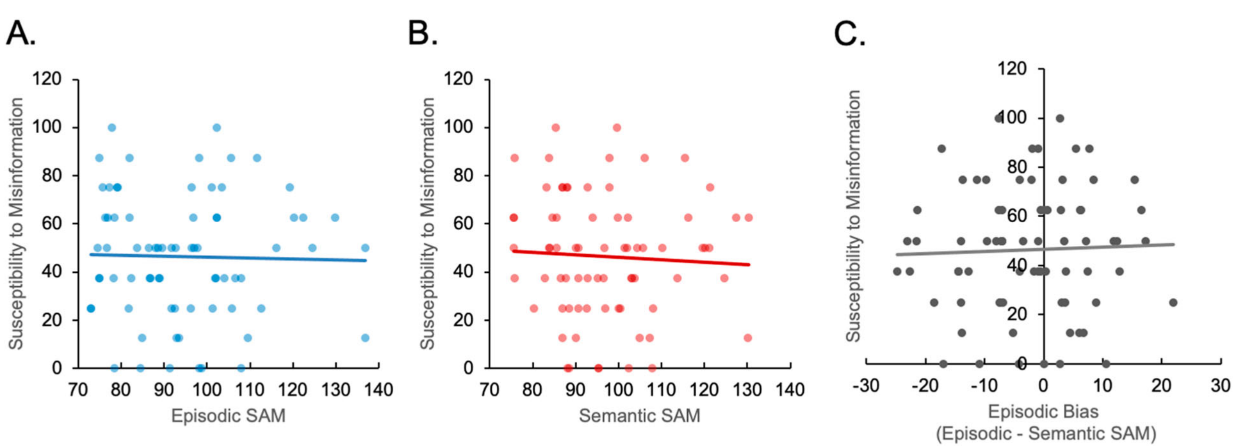

Figure 4. Correlations between susceptibility to misinformation (memory accuracy on misleading trials) and self-reported trait mnemonics on the Survey of Autobiographical Memory (SAM). (A) Relationship between susceptibility to misinformation and episodic factor score from the SAM. (B) Relationship between susceptibility to misinformation and semantic factor score from the SAM. (C) Relationship between susceptibility to misinformation and a bias towards an episodic retrieval style (episodic bias; episodic factor score – semantic factor score).

were a subset of those previously reported in a larger study by Karanian and colleagues (2020) who had completed a resting-state fMRI scan. The study was approved by the Institutional Review Board at Tufts University and all participants provided written informed consent.

Procedure

Behavioural methods

The misinformation procedure has been previously described in Karanian and colleagues (2020) and mirrors the procedure used in Study 1, with the following differences due to the constraints of MRI imaging. First, participants viewed the video of the witnessed event and took the initial memory test outside of the scanner, and then completed the audio narrative and final memory test portions of the procedure inside the scanner. Second, there was no filler task between the initial memory test and the audio narrative. Instead, participants moved into the scanner between the initial memory test and the audio narrative, resulting in a similar time period elapsing between these phases of the experiment compared to Study 1. Third, participants listened to an audio narrative recounting the witnessed event which consisted of 130 sentences (24 critical, 106 filler) separated by a jittered interstimulus interval (4-8s). Critical sentences were separated by at least three filler sentences that were not probed in the memory tests. Fourth, during the memory tests, participants were given 3s to indicate their level of confidence on an ordinal scale that ranged from 1–4 with 4 representing high confidence and 1 representing guess/low confidence, using one of four keys on a button box. Finally, a subset of participants ($n = 32$) also received a warning either before or after the audio narratives that the accuracy of the audio narrative could not be verified. In the current study, our primary analysis collapsed across all participant groups to increase power. However, we also report separate analysis restricted to participants who did not receive a warning to control for potential effects of warning.

MRI methods

Resting state scan. Participants completed a high-resolution structural scan as well as a 6.5-min resting-state scan, during which they were instructed to rest quietly with their eyes open and fixated on a white crosshair. Task-based functional scans during the audio narrative and final memory test were also collected as part of a separate study (Karanian et al., 2020).

MRI data collection and preprocessing. Structural and functional images were acquired on a Siemens 3 T Magnetom Prisma Fit scanner (Siemens Medical) with a 32-channel head coil at the Massachusetts Institute of Technology Athinoula A. Martinos Imaging Center. Resting-state functional data were acquired using a T2*-weighted EPI sequence (40 axial slices, TR = 1,500 ms, TE = 30 ms, flip angle = 61°, field of view = 210 × 210 mm, slice thickness = 3 mm). High-resolution structural images of the whole brain were acquired using a T1-weighted, rapid gradient echo- pulse sequence (MPRAGE; TR = 1,800 ms, TE = 2.36 ms, flip angle = 8°, field of view = 250 × 250 mm, slice thickness = 0.87 mm; 208 slices, 0.9 × 0.9 × 0.9 mm resolution).

Image preprocessing and data analysis were performed using SPM12 (Wellcome Department of Cognitive Neurology, London, UK) and the CONN toolbox (Whitfield-Gabrieli & Nieto-Castanon, 2012) standard preprocessing pipeline which includes segmentation, slice time correction, motion correction, coregistration, outlier identification, and spatial normalisation into MNI space. Spatial smoothing was applied using an isotropic Gaussian kernel of 4 mm FWHM. A band pass filter (0.02–0.08 Hz) was applied to the functional data to minimise the influence of physiological, head-motion and other noise sources. See the CONN toolbox website for details regarding individual steps in the preprocessing pipeline (https://web.conn-toolbox.org/fmri-methods/preprocessing-pipeline#h.p_jlSegaTEhy9a).

Data analysis

Behavioural analysis. Recognition memory performance (proportion correct) was calculated by dividing the number of test trials in which participants selected the correct video detail within each trial type (consistent, neutral, misleading) by the total number of trials for that given trial type (consistent, neutral, misleading). Susceptibility to misinformation was defined as memory accuracy on misleading trials. To test whether memory accuracy differed across trial types, memory accuracy was for each trial type first entered into ANOVA. Follow-up pairwise comparisons tested for memory accuracy differences between misleading trials and the other trial types (consistent, neutral).

fMRI analysis. Whole brain resting-state functional connectivity (rsFC) maps were computed using the CONN toolbox. Separate MTL seed regions were defined for the bilateral parahippocampal gyrus and the bilateral hippocampus using the Automated Anatomical Labeling (AAL) atlas. Whole-brain connectivity with the parahippocampal gyrus was of primary interest given prior literature associating PHG with context reinstatement during memory retrieval and accurate memory performance after exposure to misinformation (Karanian et al., 2020; Sheldon et al., 2016; Staresina et al., 2012; Stark et al., 2010). Hippocampal functional connectivity was also computed given prior evidence of hippocampal orchestration of memory reactivation and cortical reinstatement during misinformation tasks (e.g., Karanian et al., 2020; Trelle et al., 2020). Average time course data from voxels within each seed region were used as regressors of activity in voxels across the whole brain. A Fisher z-transformation was applied to maps of seed-region connectivity for second-level analysis and general linear models were used to examine the relationship between susceptibility to misinformation and the strength of seed-to-voxel rsFC. Clusters whose rsFC positively correlated with memory accuracy in the face of misinformation were extracted. The voxel-wise threshold was set to $p < .005$ with a cluster-size p-FDR corrected threshold of $p < .05$.

Results

Behavioural results

As shown in Figure 5(A), a strong misinformation effect was observed on the final memory test. ANOVA confirmed that memory accuracy differed across trial types (consistent, neutral, control; $F(2, 92) = 26.51$, $p < 0.001$, $\eta_p^2 = 0.37$) and that memory accuracy was reduced for misleading trials compared to both neutral trials (t (46) = 5.16, $p < 0.001$, $d = 0.75$, 95% CI [0.43, 1.07]) and consistent trials (t (46) = 6.18, $p < 0.001$, $d = 0.90$, 95% CI [0.56, 1.24]). As shown in Figure 5(B), susceptibility to misinformation (memory accuracy on misleading trials) varied sizably across individuals, ranging from a magnitude of 0 to 1.0. Post-hoc analysis indicated susceptibility to misinformation was not related to general memory performance (accuracy on consistent trials that were accurately described in the narrative; $r(45) = -.06$, $p = .71$), suggesting that susceptibility to misinformation did not simply reflect overall memory performance.

Intrinsic functional connectivity results

We hypothesised that protection from misinformation would be associated with stronger intrinsic functional connectivity between the MTL and posterior cortical regions involved in reactivation of visual details during memory retrieval. Consistent with this hypothesis, memory accuracy on misleading trials was positively associated with stronger functional connectivity between the bilateral parahippocampal gyrus (PHG) and cortical regions in the occipital lobe (Table 1; Figure 6). This pattern included two peaks in the left occipital gyrus (BA19) and one peak in the right occipital gyrus (BA18). A strikingly similar pattern was observed when the bilateral hippocampus was used as the seed region. Specifically, connectivity between the hippocampus and left occipital gyrus (BA19) was positively associated with memory accuracy on misleading trials (Table 1; Figure 7). Given that behavioural performance was measured as part of a larger study in which some participants received a warning about the veracity of the post-event information, it is possible that the current results could be influenced by the effect of warning on memory accuracy. To address this concern, follow-up analysis examined MTL connectivity in a subgroup of participants who did not receive a warning about the veracity of the post-event information. Although these results should be interpreted with caution given the low sample size, protection from misinformation was again positively associated with stronger PHG-occipital (BA18) functional connectivity (see Supplemental Table 1). Together, these results suggest that intrinsic functional connectivity between the MTL and posterior visual processing regions is associated with protection from misinformation.

Discussion

Accumulating evidence suggests that memory distortion due to misinformation reflects faulty reconstructive processes during memory retrieval. The current experiments investigated whether an individual's susceptibility to misinformation reflects stable underlying factors related to memory retrieval. In Study 1, we report for the first time the existence of substantial individual variability in susceptibility to misinformation in the context of repeated memory retrieval, when the misinformation effect is most pronounced. While this variability was not related to an individual's tendency to adopt an episodic versus semantic retrieval style during remembering (trait mnemonics), Study 2 found a significant association between individual variability in susceptibility to misinformation and intrinsic network connectivity in the brain. Specifically, stronger resting-state functional connectivity in MTL networks known to coordinate memory reactivation during event retrieval was associated with better protection from misinformation. These results reveal that while memory distortion is a universal property of our reconstructive memory system, susceptibility to misinformation varies at the individual level and may depend on one's ability to re-express perceptual information associated with an original event during memory retrieval.

Susceptibility to misinformation is considered a universal property of our malleable memory system, a system that routinely incorporates schema-consistent information into memory during encoding and pieces together details from the past during memory retrieval (Schacter et al., 2011). While it is unlikely that one could ever be completely immune to memory distortion (Patihis, 2018), recent evidence suggests that the magnitude of the misinformation effect differs across individuals and can be modulated by external factors such as warning (Loftus, 2005). For example, Karanian and colleagues (2020) found that providing individuals with a warning about the threat of misinformation significantly reduces the misinformation effect, even in the context of repeated memory retrieval when suggestibility is enhanced. This protective effect of warning was associated with changes in neural activity during memory retrieval, including enhanced reactivation of sensory regions associated with the original visual event (occipital cortex) and reduced reactivation of sensory regions associated with the misleading information (auditory cortex). This suggests that while all people are likely susceptible to misinformation, the magnitude of the misinformation effect can be reduced by factors that influence event reconstruction during memory retrieval. The current study builds upon this work to demonstrate that susceptibility to misinformation within this paradigm can

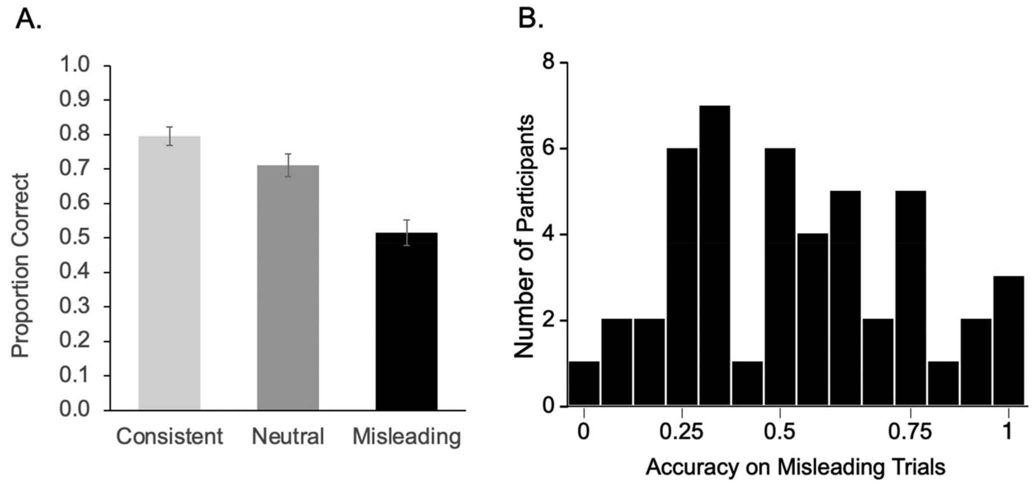

Figure 5. Behavioural results from Study 2. (A) Results from the final memory test. Memory accuracy (proportion correct) within each trial type (consistent, neutral, misleading). Error bars indicate SEM. (B) Individual variability in susceptibility to misinformation (memory accuracy on misleading trials).

also be influenced by stable, intrinsic factors related to memory reactivation that vary across individuals.

In Study 1, we first demonstrate the presence of substantial individual variability in susceptibility to misinformation in the context of repeated memory retrieval. Prior work has demonstrated that susceptibility to misinformation is potentiated when individuals are tested on their memory for an event before being exposed to misinformation (Chan et al., 2009; Chan et al., 2017; Thomas et al., 2010), a situation that is common in everyday remembering and eyewitness memory. While individual differences in misinformation susceptibility have been demonstrated in a handful of prior studies (see Nichols & Loftus, 2019), an important open question was whether such variability is present in repeated retrieval contexts. The results from Study 1 demonstrate that this is indeed the case. Striking heterogeneity in susceptibility to misinformation was observed in the context of repeated memory retrieval, with some individuals incorporating all misleading details into memory while others not incorporating any misleading details at all.

Given this finding, our next goal was to investigate whether individual variability in misinformation susceptibility relates to stable underlying cognitive or neural factors. Prior research has found that susceptibility to misinformation relates to individual difference factors such as age, personality, and low intelligence combined with poor perceptual abilities (e.g., Brackmann et al., 2016; Zhu et al., 2010). However, significant individual difference correlates of misinformation susceptibility have not always been observed (Nichols & Loftus, 2019). Here, we specifically targeted individual difference variables related to memory retrieval and the tendency to recover vivid sensory details from past episodes during remembering. This was motivated by current theoretical models of memory distortion, which attribute misinformation errors to faulty reconstructive processes during memory retrieval and the failure to reactivate visual details from accurate versus misleading sources of information (e.g., Ayers & Reder, 1998; Stark et al., 2010).

We first examined whether one's memory retrieval style represents a stable factor related to misinformation susceptibility (Study 1). Prior work has established that a tendency to recover detailed episodes (episodic retrieval style) versus more abstract, schematic information (semantic retrieval style) is associated with intrinsic functional connectivity in MTL networks that support the reactivation of visual details during remembering (Sheldon et al., 2016). Specifically, stronger connectivity between the parahippocampal gyrus (PHG) and occipital cortex at rest was positively associated with an episodic bias during memory retrieval as measured by the Survey of Autobiographical Memory (SAM). If the ability to strongly reactivate sensory-specific details about an original event protects individuals from misinformation, we predicted that those who report an episodic bias during memory retrieval would demonstrate better memory accuracy in face of misinformation. Although no such association was found in the present study, it is important to note that the current study used the short form version of the SAM which may have reduced sensitivity to pick up on significant individual variability. Future work could use the long form version of the SAM or combine the SAM with

Table 1. Peak regions of MTL connectivity correlating with protection from misinformation

			MNI Coordinates		
Region	BA	*k*	*x*	*y*	*z*
PHG Seed					
L. Occipital Cortex	19	414	−22	−78	18
L. Occipital Cortex	19	97	−38	−64	−14
R. Occipital Cortex	18	90	24	−90	06
Hippocampus Seed					
L. Occipital Cortex	19	175	−50	−80	−16

Note: BA = Brodmann Area, *k* = cluster size.

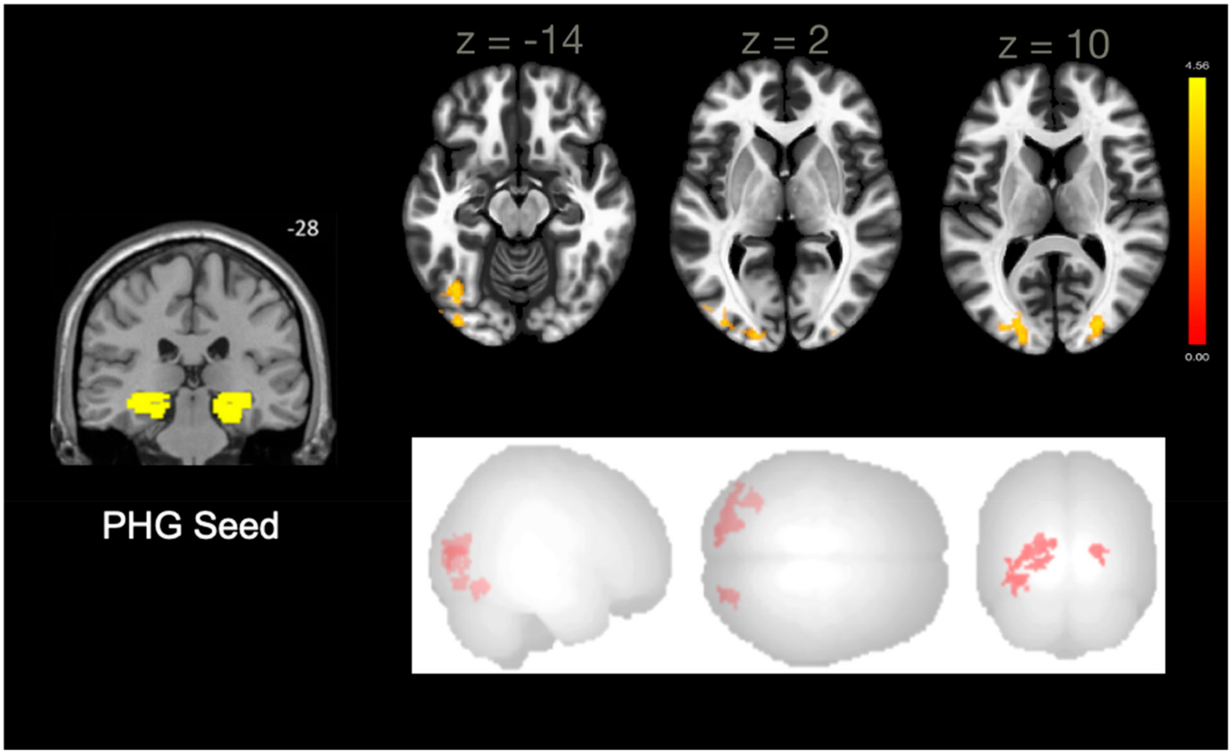

Figure 6. Whole brain functional connectivity maps using the bilateral parahippocampal gyrus (PHG) as a seed. Stronger intrinsic functional connectivity between PHG and visual cortical regions was positively associated with protection from misinformation (memory accuracy on misleading trials). Anatomically defined PHG seed is depicted in yellow (left). PHG connectivity to occipital cortex depicted on axial brain slices (top row) and on the whole brain (bottom row).

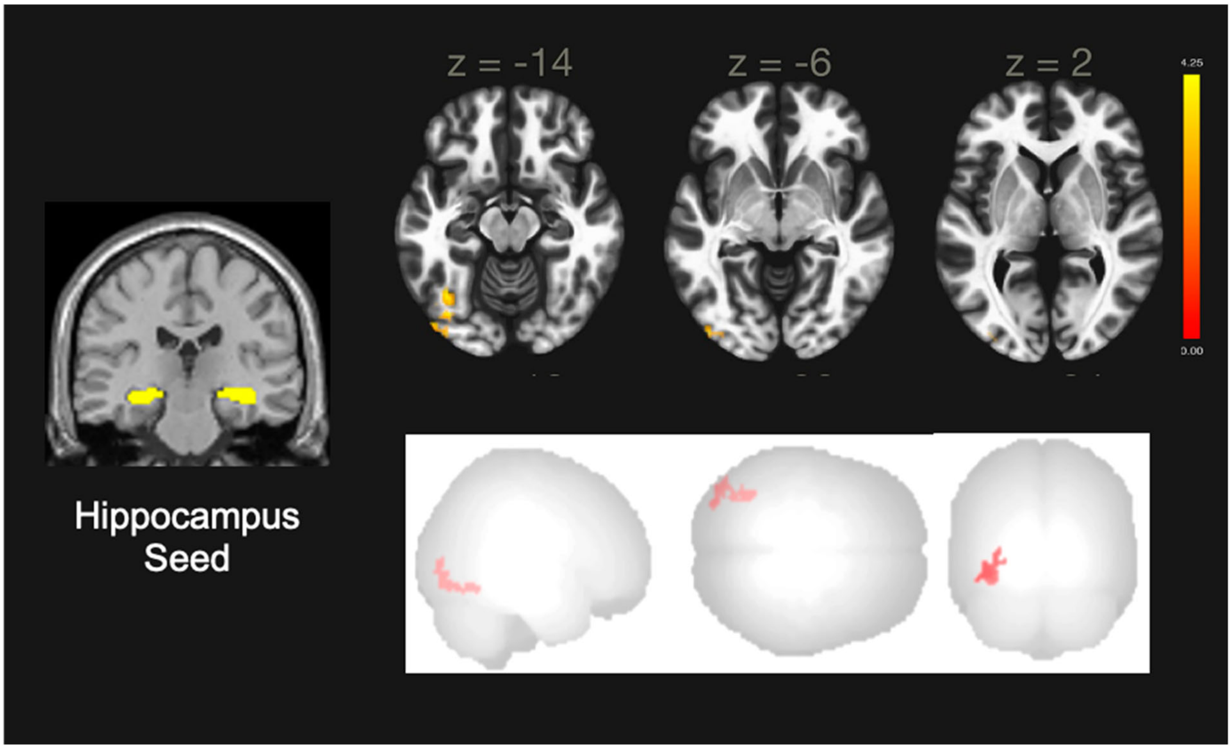

Figure 7. Whole brain functional connectivity maps using the bilateral hippocampus as a seed. Stronger intrinsic functional connectivity between the hippocampus and visual cortical regions was positively associated with protection from misinformation (memory accuracy on misleading trials). Anatomically defined hippocampal seed is depicted in yellow (left). Hippocampal connectivity to occipital cortex depicted on axial brain slices (top row) and on the whole brain (bottom row).

other measures of memory retrieval style to further investigate the relationship to memory accuracy (e.g., Raes et al., 2007; Williams & Broadbent, 1986). It is also possible that such self-report measures of trait mnemonics may not capture the components of memory retrieval most related to sensory reactivation and susceptibility to misinformation (Setton et al., 2022). Thus, in Study 2 we next examined individual variability in underlying neural mechanisms related to memory reactivation more specifically.

Recently, Nichols and Loftus (2019) proposed that investigating neural measures previously associated with true and false memories may provide important insight into the factors underlying trait susceptibility to misinformation. In line with this proposal, Study 2 found that susceptibility to misinformation was related to intrinsic functional connectivity in MTL networks known to coordinate memory reactivation during event retrieval (Staresina et al., 2012; Trelle et al., 2020). Prior neuroimaging studies have highlighted the importance of task-based activity in the MTL and occipital cortex for memory accuracy in the face of false or misleading information (Baym & Gonsalves, 2010; Karanian et al., 2020; Okado & Stark, 2005; Shao et al., 2022; Shao et al., 2023; Stark et al., 2010; Ye et al., 2016; Zhu et al., 2019). Here, we extend this work to demonstrate that connectivity in MTL-occipital networks at rest is associated with protection from misinformation. Interestingly, we found that this pattern was specific to network connectivity between the MTL and visual processing regions in the occipital cortex, regions that have been identified in both task-based misinformation studies (e.g., Karanian et al., 2020; Stark et al., 2010) as well as resting-state connectivity studies associated with episodic retrieval style (Sheldon et al., 2016). The specificity of MTL connectivity to the occipital lobe in the current results suggests that connectivity to cortical regions involved in visual reactivation may be particularly important for memory accuracy in the face of misinformation. For example, individuals who have stronger intrinsic connectivity in these networks may be able to more easily or readily recover accurate visual details from an original event when remembering. In support of this possibility, post-hoc analysis revealed that participants who demonstrate stronger MTL-occipital connectivity at rest also demonstrate stronger reactivation of occipital cortex during memory retrieval (reported in Karanian et al., 2020) (Supplemental Table 2). Such a proposal would complement and extend theories of memory distortion which attribute misinformation errors to faulty reactivation of inaccurate rather than accurate sources of information (Ayers & Reder, 1998; Karanian et al., 2020; Stark et al., 2010).

While the results of Study 2 provide novel evidence that stable neural connectivity profiles at rest are associated with protection from misinformation, there are several limitations that should be addressed in future work. First, the participants in Study 2 represent a subgroup of the participants who participated in a larger study that examined the effect of warning on susceptibility to misinformation (Karanian et al., 2020). All participants in that larger study who had resting-state data were included in the current study to increase power. However, it is possible that the current results could be influenced by the inclusion of some participants who received a warning prior to exposure to misinformation, given that warnings have been shown to reduce the magnitude of the misinformation effect (Karanian et al., 2020; Loftus, 2005). Thus, the inclusion of warned participants in Study 2 could have added noise to our behavioural measure and reduced the strength of the association with neural connectivity. Despite this limitation, a positive association was still observed between susceptibility to misinformation and the magnitude of MTL network connectivity. In addition, the positive association between MTL-occipital connectivity and memory performance remained when analysis was restricted to a subgroup of participants who did not receive a warning (Supplemental Table 1). Nevertheless, an important goal of future research will be to replicate the current results in a new, larger sample of participants.

It will also be important for future work to investigate whether the present MTL connectivity results extend to other misinformation and false memory paradigms more broadly. Currently, the degree to which the observed brain–behavior associations reflect item-level variance or other aspects of the current paradigm is unclear. For example, does MTL-visual connectivity still predict memory accuracy when the original witnessed event is presented in an auditory rather than a visual modality (e.g., "earwitness" paradigms)? Future work should also investigate the degree to which the neural connectivity patterns observed in Study 2 reflect stable, trait-like variables. While a novel aspect of the current study was the measurement of functional connectivity at rest versus during the memory task, it is known that individuals continue to reactivate memories even at rest (e.g., Tambini & Davachi, 2013). Given that participants in our study always performed the misinformation memory paradigm and the resting-state scan within the same session, the degree to which the observed MTL functional connectivity results reflect intrinsic connectivity patterns that are stable over time versus more active memory reactivation following a memory test is unknown. Future work could investigate this possibility by measuring resting-state functional connectivity in a separate session or at different time periods before or after the memory test.

Future work could also investigate the degree to which other factors such as age or gender influence the association between MTL connectivity and susceptibility to misinformation. For example, accumulating evidence suggests that older adults may be particularly susceptible to misinformation (Mitchell et al., 2003; Multhaup et al., 1999). However, substantial age-related variability in susceptibility to misinformation has also been observed (e.g., Gabbert et al., 2004; Roediger & Geraci, 2007). An important outstanding question is whether age-related changes in susceptibility to misinformation reflect variability in interregional functional connectivity (Sala-Llonch et al., 2015), particularly reduced connectivity between the MTL and posterior cortical regions involved in visual processing (Dennis et al., 2008).

Conclusion

The current results provide novel insight into the underlying mechanisms that render individuals more or less susceptible to memory distortion following exposure to misinformation. Importantly, while memory errors due to misinformation are a universal property of our reconstructive memory system, the current results reveal that intrinsic properties of MTL network connectivity play an important role in the magnitude of the misinformation effect. The finding that connectivity associated with memory performance involved MTL-occipital networks known to coordinate memory reactivation supports and extends theories of memory distortion that attribute misinformation memory errors to reduced reactivation of sensory cortex associated with an original event (Karanian et al., 2020; Stark et al., 2010). In sum, these results suggest that intrinsic network connectivity in brain regions associated with memory reactivation may be an important factor in determining an individual's susceptibility to misinformation.

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Data availability statement

The data that support the findings of Study 1 and Study 2 are available on request from the corresponding author, ER. The data that support the findings of Study 2 are partially derived from resources available in the OSF database (DOI: 10.17605/https://osf.io/WGN83/).

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