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Journal
Brain Structure and Function, 221(8)

ISSN
1863-2653

Authors
Zhu, Bi
Chen, Chuansheng
Loftus, Elizabeth F
et al.

Publication Date
2016-11-01

DOI
10.1007/s00429-015-1145-1

Peer reviewed

Brain Struct Funct (2016) 221:4045–4057
DOI 10.1007/s00429-015-1145-1

ORIGINAL ARTICLE

Hippocampal size is related to short-term true and false memory, and right fusiform size is related to long-term true and false memory

Bi Zhu[1,2,3] · Chuansheng Chen[4] · Elizabeth F. Loftus[4] · Qinghua He[1,2] · Xuemei Lei[1,2] · Qi Dong[1,2] · Chongde Lin[1,2,3]

Received: 20 April 2015 / Accepted: 5 November 2015 / Published online: 19 November 2015

Abstract There is a keen interest in identifying specific brain regions that are related to individual differences in true and false memories. Previous functional neuroimaging studies showed that activities in the hippocampus, right fusiform gyrus, and parahippocampal gyrus were associated with true and false memories, but no study thus far has examined whether the structures of these brain regions are associated with short-term and long-term true and false memories. To address that question, the current study analyzed data from 205 healthy young adults, who had valid data from both structural brain imaging and a misinformation task. In the misinformation task, subjects saw the crime scenarios, received misinformation, and took memory tests about the crimes an hour later and again after 1.5 years. Results showed that bilateral hippocampal volume was associated with short-term true and false memories, whereas right fusiform gyrus volume and surface area were associated with long-term true and false memories. This study provides the first evidence for the structural neural bases of individual differences in short-term and long-term true and false memories.

Keywords Individual differences · Memory distortions · Misinformation · MRI

Introduction

Memory is malleable. Eyewitness memory for an event can be tainted after exposure to post-event misinformation. Research has also shown substantial individual variations in true and false memories after exposure to misinformation (Loftus 2005). Therefore, there is a keen interest in identifying specific brain regions (e.g., the hippocampus) that are associated with individual differences in false memories.

The hippocampus, a brain structure located in medial temporal lobe, plays an essential role in the creation of false memory in both animals and humans (Ramirez et al. 2013; Schacter et al. 2011). Both functional and structural neuroimaging studies have suggested that the human hippocampus may be a key region for true and false memories from misinformation. First, previous fMRI studies showed that the strength of hippocampal activations during the encoding of the original event and misinformation predicted subsequent true or false memory (Baym and Gonsalves 2010; Okado and Stark 2005), and that greater hippocampal activations during retrieval were related to both true and false memory (Stark et al. 2010). In addition, greater hippocampal activation for persistent false memory

Electronic supplementary material The online version of this article (doi:10.1007/s00429-015-1145-1) contains supplementary material, which is available to authorized users.

✉ Bi Zhu
psyzhubi@163.com

✉ Elizabeth F. Loftus
eloftus@uci.edu

1 State Key Laboratory of Cognitive Neuroscience and Learning and IDG/McGovern Institute for Brain Research, Beijing Normal University, Beijing 100875, China

2 Center for Collaboration and Innovation in Brain and Learning Sciences, Beijing Normal University, Beijing 100875, China

3 Institute of Developmental Psychology, Beijing Normal University, Beijing 100875, China

4 Department of Psychology and Social Behavior, University of California, Irvine, 2393 Social Ecology II, Irvine, CA 92697, USA

was observed during the encoding of misinformation from other co-observers or computer (Edelson et al. 2011).

Second, several structural neuroimaging studies of healthy subjects found positive correlations between hippocampal volume (HPV) and episodic memories (Ashtari et al. 2011; Gur et al. 2000; Molnar and Keri 2014; Pohlack et al. 2014), although two earlier studies reported negative HPV–memory correlations (Chantôme et al. 1999; Foster et al. 1999). Specifically, Gur et al. (2000) reported that higher hippocampal volumes were associated with better verbal and spatial memories measured by the California Verbal Learning Test (CVLT) and the Wechsler Memory Scale (WMS-R). The positive association between hippocampal volume and performance on the CVLT was replicated by Ashtari et al. (2011) and Pohlack et al. (2014). The positive association between hippocampal volume and performance on WMS-R was replicated by (Molnar and Keri 2014). However, negative correlations between hippocampal volume and memory were reported in two earlier studies, one using a delay story recall task (Foster et al. 1999) and the other using stem-cued word recall task (Chantôme et al. 1999).

Third, studies using various clinical samples also reported hippocampal functional–structural correlates of memory (Gimenez et al. 2005; Powell et al. 2007; Putcha et al. 2011). For example, in a study of adolescents who were born premature, Gimenez et al. (2005) found that right hippocampal volume (based on structural MRI data) was positively correlated with right hippocampal activation (based on functional MRI data) during a face–name learning task, which was in turn positively correlated with memory performance. In a study of patients with temporal lobe epilepsy due to unilateral hippocampal sclerosis, Powell et al. (2007) found positive correlations between left hippocampal volume and word encoding-related left hippocampal fMRI activation, and between right hippocampal volume and picture encoding-related right hippocampal fMRI activation. In contrast, negative correlations were reported between hippocampal volume and hippocampal fMRI activation during a face–name memory task in elderly patients with mild cognitive impairment (Putcha et al. 2011; Sandstrom et al. 2006). These results indicate that hippocampal grey matter volume variation plays a role in differential hippocampal functional activation during memory tasks, although the direction of the correlations may depend on factors such as age of the subjects.

In sum, there is a preponderance of evidence suggesting a positive association between hippocampal volume and memory measured with short-delay tests such as CVLT and WMS-R, where the short delay ranged from minutes to 2 weeks. Indeed, the crucial role of the hippocampus in memory is time-limited (Squire et al. 2010). Memories are thought to become gradually independent of the hippocampus and increasingly dependent on the cortical regions (Frankland and Bontempi 2005; Kirwan et al. 2008; Nadel and Hardt 2011).

The right fusiform gyrus, located on the ventromedial surface of the right temporal and occipital lobes, plays a role in preventing the formation of false memories (i.e., mistaking similar objects for those seen at encoding) (Garoff et al. 2005). It has been found that the right fusiform is functionally more sensitive to perceptual changes than is the left fusiform in an fMRI study (Simons et al. 2003). Relatedly, the right fusiform shows the expertise effect for visual perception of faces, bodies, cars, birds, and well-learned objects in several fMRI studies (Gauthier et al. 1999, 2000; Kanwisher et al. 1997; Peelen and Downing 2007). Evidence for the right fusiform's involvement in specific long-term memory of persons and scenes also came from lesion studies. For example, a patient with lesion to the right fusiform often misidentified her husband as her sister and referred to her real home as a rented replica (Hudson and Grace 2000).

Structural neuroimaging studies also showed that right fusiform gyrus volume was associated with memory and illusion (Dickey et al. 2003; Nestor et al. 2007; Onitsuka et al. 2003, 2006; Trontel et al. 2013). For example, schizophrenic patients with more severe clinical symptoms were found, in separate studies, to have smaller volumes of right fusiform gyrus (Dickey et al. 2003) and less false memory (Paz-Alonso et al. 2013), suggesting that right fusiform gyrus volume might be associated positively with false memory. In terms of true memory, smaller volumes of the right fusiform gyrus have been associated with better delayed face memory in middle-aged adult patients with schizophrenia (Nestor et al. 2007; Onitsuka et al. 2003), but worse delayed face memory in children with autism (Trontel et al. 2013). In further support of the connection between the right fusiform volume and face memory, researchers found negative correlations between right posterior fusiform gyrus volumes and N170 amplitudes in response to images of faces in schizophrenia patients (Onitsuka et al. 2006).

Interestingly, one study showed that volumes of the fusiform gyrus and hippocampus were independently associated with the level of cognitive impairment in patients with Alzheimer's disease (Convit et al. 1997). Specifically, the fusiform gyrus volume was smaller for dementia (DAT) patients as compared with patients with minimal cognitive impairment (MCI) patients and normal controls, whereas the hippocampal volume was smaller for DAT and MCI patients as compared with normal controls. Regression analysis found that the volumes of the hippocampus and the fusiform gyrus both made independent contributions to the accuracy of classification of MCI and

DAT patients. Taken together, the correlation between right fusiform gyrus volume and true memory might be negative in schizophrenic young and middle-aged adults, but positive in autistic children and the elders with Alzheimer's disease. These results also suggest that both the right fusiform gyrus and the hippocampus may contribute to individual differences in long-term true and false memories.

In addition to the hippocampus and fusiform gyrus, the parahippocampal gyrus located between the two needs to be considered. Previous functional imaging studies suggest that the parahippocampal gyrus also plays a role in true and false memories, but the results were inconsistent across studies. For example, some studies found greater parahippocampal activation for true memory than false memory (Cabeza et al. 2001; Okado and Stark 2003), but recent studies reported greater activity of the parahippocampal cortex for false memory (Edelson et al. 2014; Karanian and Slotnick 2014). Researchers also found that the activity of the left parahippocampal cortex was related to false memory using the misinformation paradigm (Okado and Stark 2005; Stark et al. 2010). For the relation between parahippocampal gyrus volume and true memory, one study reported a positive correlation using delayed recall in AD patients, but not in healthy controls (Kohler et al. 1998), but another study reported no significant correlation between parahippocampal gyrus volume and delayed verbal and spatial recall in either AD patients or healthy controls (de Toledo-Morrell et al. 2000).

The above literature review led us to hypothesize that structural variations in the hippocampus and the right fusiform gyrus as well as the parahippocampal gyrus would be associated with individual differences in true and false memories arising from misinformation. Due to the time-limited role of the hippocampus in memory, we hypothesized that hippocampal volume would be associated positively with short-term (i.e., within an hour) true memory and negatively with false memories, but not with long-term memories (i.e., after 1.5 years). Because right fusiform gyrus is involved in true and false memories (especially for specific long-term memory of persons and scenes), we hypothesized that right fusiform gyrus volume would be associated with both short- and long-term true and false memories. Unlike the hippocampus, right fusiform gyrus volume was expected to be associated negatively with true memory and positively with false memory based on previous results (Dickey et al. 2003; Nestor et al. 2007; Onitsuka et al. 2003; Paz-Alonso et al. 2013). Finally, we hypothesized that parahippocampal gyrus volume would be associated positively with true memory and negatively associated with false memory. Moreover, we hypothesized that right fusiform gyrus and hippocampal volumes would make independent contributions to predicting true and false memories.

To test these hypotheses, we used structural MRI scanning to measure the hippocampus, fusiform gyrus, and parahippocampal gyrus in a sample of healthy young adults ($N = 205$). All these subjects also participated in a misinformation task. Specifically, they were shown slides depicting crime scenarios, then received misinformation about the events half an hour later, and finally completed a recognition task at two time points (i.e., a "short-term" period of within an hour after the events and a "long-term" period of 1.5 years later) (Fig. 1a). We examined associations between the volumes of these brain regions of interest and reports of true and false memories. In addition, since cortical volume is a combination of cortical surface area and cortical thickness, we also measured the surface area and thickness of fusiform and parahippocampal gyrus, and explored their correlations with memory.

Materials and methods

Participants

Participants were 205 healthy Chinese college students (mean age 20.45 years, SD 0.88; 59 % female, 98 % right handed) with valid brain imaging and memory performance data at Time 1 (in an hour) and at Time 2 (after 1.5 years). They had normal or corrected-to-normal vision and reported no history of psychiatric or neurological diseases, head injuries, or stroke/seizure. Written informed consent was obtained from each participant after a full explanation of the study procedure. This study was approved by the Institutional Review Board (IRB) of Beijing Normal University, China. Handedness did not influence any results in the current study, therefore we included all subjects in the analysis. The current study sample ($N = 205$) was a part of a larger sample in our previous behavioral study on long-term false memory ($N = 342$, mean age 20.49 years, SD 0.99; 56 % female, 97 % right handed) (Zhu et al. 2012). To assess potential attrition biases, we compared subjects included in the current sample with the non-included subjects in terms of their age, sex, and their scores on memory tests at Time 1 and at Time 2, and found no significant differences (t ranged from 0.53 to 1.58; all $p > 0.05$).

Behavioral assessments

The behavioral assessment involved four stages: events, narrations, a memory test at Time 1, and a memory test at Time 2. We measured misinformation false memory using previously established and reliable materials (Okado and

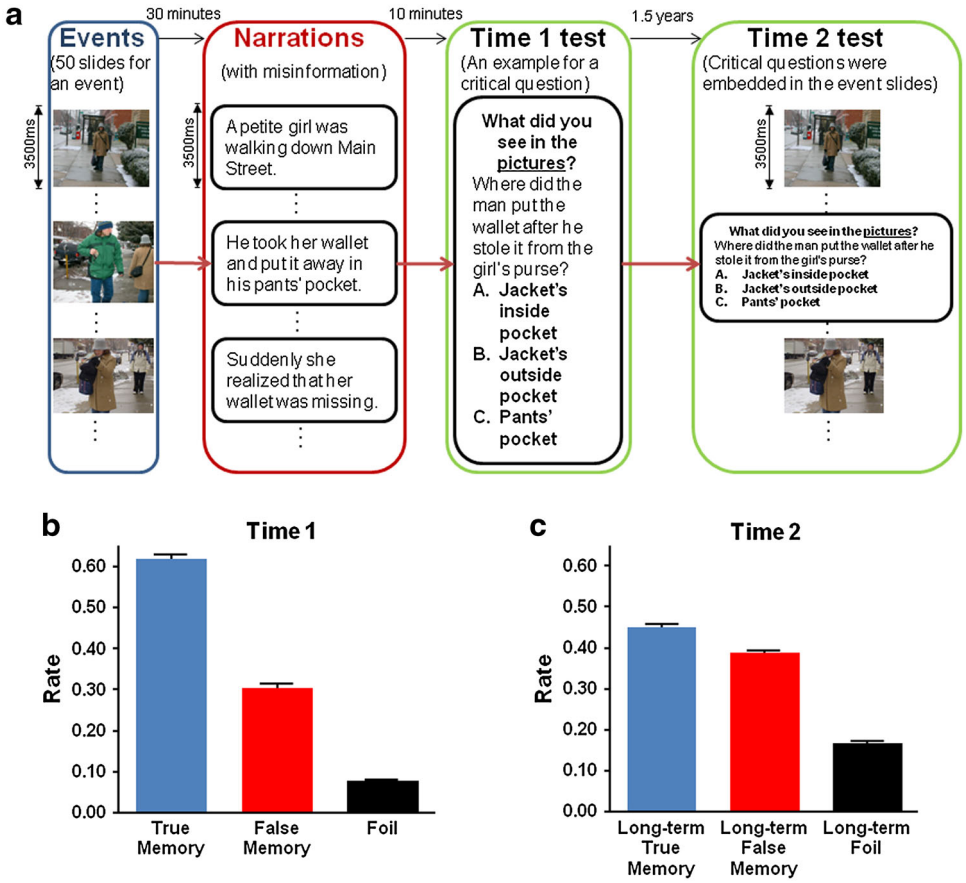


Fig. 1 Experimental design and behavioral results. **a** Participants saw two separate crime scenarios that unfolded in slideshows consisting of 50 images each, including 12 critical slides that would be inaccurately described in the subsequent narrations. Half an hour later, they read two narrations consisting of 50 sentences each, including 12 misinformation and 38 accurate descriptions. Ten minutes later, they took the memory recognition test at Time 1 (i.e., an hour after they saw the original events). After 1.5 years, they took the same memory recognition test again while the critical questions were embedded in the slides at Time 2. A sample critical slide (i.e., jacket's outside pocket), its narration with misinformation (i.e., pants' pocket), its critical question at Time 1 and Time 2 were linked by *red arrows*. The endorsement rates of the original (e.g., jacket's outside pocket) and misinformation (e.g., pants' pocket) items represented true and false memories, respectively. **b** Recognition memory test performance at Time 1 (means and standard errors) revealed false memory was higher than foil. **c** Recognition memory test performance at Time 2 (means and standard errors) revealed long-term false memory was higher than long-term foil

Stark 2005; Patihis et al. 2013; Stark et al. 2010). In the first stage, all participants saw two separate events, one depicting a girl's wallet being stolen by a seemingly nice man and the other depicting a man breaking into a car and stealing things from it. For each event, 50 digital color slide images were presented in sequence. Each slide was shown for 3500 ms with an inter-slide interval of 500 ms. Of the 50 slides that comprised each event, 12 were critical slides that would be inaccurately described in the subsequent narrations (which are described below). To attain a balanced design, two versions of each critical slide image were generated, which were counterbalanced between participants. For example, one participant may see a man put the wallet in his jacket's outside pocket and would read the misinformation at the second stage that he put the wallet in his pants' pocket (as shown in Fig. 1a), whereas another participant may see the man put the wallet in his pants' pocket and would read the misinformation at the second stage that he put the wallet in his jacket's outside pocket.

In the second stage, participants read two narratives, one pertaining to each of the events they had seen 30 min ago. The narratives consisted of one sentence for each slide image describing the scene depicted in the image. For each event, 50 sentences were presented, including 12 inaccurate descriptions (i.e., misinformation) and 38 accurate descriptions (i.e., consistent with the original picture slides). Each sentence was shown for 3500 ms with an interval of 500 ms between sentences. Participants were informed that they were to read narrations made by an eyewitness to those events, with no warning about potential discrepancies between the picture slides and the narrations.

In the third stage, participants took the memory (recognition) test after a 10 min interval (i.e., 1 h after the presentation of the original events). For the recognition test, 12 critical questions (pertaining to the critical slides) were asked for each event (i.e., "you saw the picture slides and read the narrations, please try your best to answer the following questions based on what you saw in the picture slides"). There was no explicit "warning" that narrations included misinformation. For the recognition test of each event at Time 1, the questions were presented in random order (i.e., not following the chronology of events depicted in the slides). Each question had three possible choices as answers. Choices were either a detail presented in the picture ("original item") or a detail presented in the narrations with misinformation ("misinformation item") or a new foil detail ("foil item"). For example, the participants might see a man hiding behind a door after stealing a girl's wallet and would then read in the post-event narration that he was hiding behind a tree. For the critical question "Where was the man hiding after stealing the girl's wallet?", the choices were "behind the tree" (misinformation item), "behind the door" (original item) and "behind the car" (foil). The endorsement rates of the original, misinformation, and foil items represented the "true memory", "false memory", and "foil", respectively. For the intervals between the first, second, and third stages, subjects took filler tasks which are unrelated to the current memory task.

In the fourth stage, which occurred 1.5 years later, all participants took a recognition memory test, but this time the test was embedded in the slide show. The "embedded" test was conducted in the following way: participants saw the same two 50-slide events again (with the same procedure as they were presented at Time 1), except the presentation of the slides stopped right before each critical slide. Instead of showing the critical slide, participants were simply asked what had happened in this missing critical slide and they were to answer based on what they remembered seeing in the original pictures shown 1.5 years earlier. After subject answered, the presentation of the slides continued. For these 12 critical questions in each event, their content was exactly the same as the original recognition test used at Time 1. In other words, this was a recognition test with three alternatives: original, misinformation, and foil. All these tests were self-paced and administered on computers.

Participants were debriefed at the end of the fourth stage. It should be noted that at the end of the first memory test, the participants were not told that they would be tested again 1.5 years later. Instead, as part of a larger project, these subjects were asked to complete several questionnaires and tested with many instruments at the first time and were told only that they would be contacted again in the future for more data collection.

MRI data collection and analysis

MRI scans were performed on a 3.0T Siemens Magnetom Trio scanner equipped with a standard head coil at Beijing Normal University Brain Imaging Center. Structural MRI data were acquired with the T1-weighted, three-dimensional, MPRAGE pulse sequence, using the following imaging parameters: TE 3.75 ms, TR 2530 ms, flip angle 7°; FOV 256 mm × 256 mm, voxel size $1 \times 1 \times 1.33$ mm^3, number of partitions 128. For all participants in the current study, the structural MRI data were collected on the sixth month after the completion of the first memory test. To extract volumetric measures of regions of interest (Fig. S1), MRI data were analyzed automatically with atlas-based FreeSurfer segmentation software (http://surfer.nmr.mgh.harvard.edu, version 5.0.0) (Fischl et al. 2002). Volumes of bilateral hippocampus and cortical topographical measures (including the grey matter volume, total surface area, and average thickness of left and right fusiform gyrus and parahippocampal gyrus) were generated according to the standard FreeSurfer segmentation and cortical parcellation procedures (based on the Desikan–Killiany atlas), relying upon variations in voxel signal intensities, probabilistic atlas location, and local spatial relationships between the structures (Desikan et al. 2006; Fischl et al. 2002). Previous research provided strong evidence for the reliability of anatomical indices estimated using FreeSurfer (Fischl 2012; Saygin et al. 2012). Intracranial volume (ICV), including brain tissues and other biological materials such as meninges and cerebrospinal fluid, was taken from the standard output of FreeSurfer analysis as well. Quality control of scan images and segmentation was assured by visual inspection of the whole cortex of each subject. Any inaccuracies in Talairach-transformation, skull stripping, and segmentation were manually corrected, and re-inspected.

Statistical analysis

For the behavioral data, we compared false memory with true memory and foils at Time 1 and Time 2, and calculated the correlations between memory performance at Time 1 and Time 2. For the neural correlates, we obtained partial correlations between memory indices and anatomical indices of brain regions of interest (i.e., hippocampal volume; and the volume, surface area, and thickness of the fusiform gyrus and parahippocampal gyrus) after partialling out sex, age, and ICV. Next, linear regression models were used to detect the associations between each memory index and anatomical indices of brain regions of interest, with sex, age, and ICV included as covariates. The effects of age, sex, and ICV on variables in the current study were also examined. Finally, we examined the

differences in anatomical correlates of short-term vs. long-term memories.

Results

The behavioral results indicated that the misinformation effect was significant both at Time 1 and Time 2. At Time 1 (Fig. 1b; tested in an hour), participants endorsed on average 61.52 % (SD 16.03 %) of the original items (true memory), 30.57 % (SD 16.48 %) of the misinformation item (false memory), but only 7.86 % (SD 5.01 %) of the foil items (foil). False memory was higher than foil [$t(204) = 17.79$, $p < 0.0001$], but lower than true memory [$t(204) = -13.79$, $p < 0.0001$]. At Time 2 (Fig. 1c; tested after 1.5 years) participants endorsed 45.05 % (SD 9.47 %) of the original items (long-term true memory), 38.70 % (SD 9.66 %) of the misinformation items (long-term false memory), but only 16.58 % (SD 7.46 %) of the foil items (long-term foil). Long-term false memory was higher than long-term foil [$t(204) = 22.02, p < 0.0001$], but lower than long-term true memory [$t(204) = -5.17$, $p < 0.0001$]. Comparing results of Time 1 and Time 2, true memory declined over time [$t(204) = -14.08$, $p < 0.0001$], and false memory increased [$t(204) = 6.91$, $p < 0.0001$] as did foil memory [$t(204) = 14.15$, $p < 0.0001$]. There was also evidence of consistency in true and false memories over the two time periods. After controlling for age and sex, false memories measured at the two time points were significantly correlated [$r(201) = 0.28$, $p < 0.0001$], so was the case for true memory [$r(201) = 0.23$, $p = 0.0011$], but there was no significant correlation for foils [$r(201) = 0.06, p = 0.4142$].

To examine the neuroanatomical correlates of true and false memories, anatomical indices of the brain regions of interest (i.e., bilateral hippocampus, fusiform gyrus, and parahippocampal gyrus) were selected. Table 1 shows their relationship with memory performance at Time 1 and Time 2, after controlling for age, sex, and intracranial volume (distributions of the major variables are shown in Fig. S2). As shown in Fig. 2, bilateral hippocampal volumes were positively correlated with true memory at Time 1 [$r(200) = 0.19$, $p = 0.0058$ for the left hippocampal volume; $r(200) = 0.22$, $p = 0.0015$ for the right hippocampal volume], and negatively correlated with false memory at Time 1 [$r(200) = -0.15$, $p = 0.0287$ for the left hippocampal volume; $r(200) = -0.20$, $p = 0.0048$ for the right hippocampal volume]. They were not significantly correlated with long-term true or false memory at Time 2.

As hypothesized, the volume of the right fusiform gyrus was positively correlated with false memory at both time points [$r(200) = 0.15$, $p = 0.0293$ at Time 1; $r(200) = 0.23$, $p = 0.0013$ at Time 2], and negatively correlated with true memory at both time points [$r(200) = -0.16$, $p = 0.0207$ at Time 1; $r(200) = -0.17$, $p = 0.0156$ at Time 2]. There was no significant correlation between any memory indices and left fusiform gyrus volume ($p > 0.05$).

Similar to the results for the hippocampus, left parahippocampal gyrus volume was positively correlated with true memory at Time 1 [$r(200) = 0.14$, $p = 0.0416$], and negatively correlated with false memory at Time 1 [$r(200) = -0.15$, $p = 0.0373$]. The correlations between left parahippocampal gyrus volume and long-term true or false memory at Time 2 were not significant ($p > 0.05$). In addition, the right parahippocampal gyrus volume was not correlated with any memory indices ($p > 0.05$).

Because cortical volume is a combination of cortical surface area and cortical thickness, we further examined whether one or both of these two structural indices were responsible for the above findings. For the right fusiform gyrus, the surface area was positively correlated with long-term false memory at Time 2 [$r(200) = 0.21$, $p = 0.0031$], and negatively correlated with long-term true memory at Time 2 [$r(200) = -0.19$, $p = 0.0072$], but it did not have significant correlations with memory indices at Time 1 ($p > 0.05$). Moreover, there was no significant correlation between any memory indices and right fusiform gyrus thickness or the anatomical indices of left fusiform gyrus ($p > 0.05$).

For the left parahippocampal gyrus, the thickness was positively correlated with true memory at Time 1 [$r(200) = 0.16$, $p = 0.0223$], and negatively correlated with false memory at Time 1 [$r(200) = -0.18$, $p = 0.0114$]. But there was no significant correlation between any memory indices and left parahippocampal gyrus surface area ($p > 0.05$). In addition, right parahippocampal gyrus surface area was negatively correlated with long-term true memory at Time 2 [$r(200) = -0.15$, $p = 0.0307$]. The other indices of parahippocampal gyrus were not correlated with memory indices ($p > 0.05$). Six correlations (i.e., those between left and right hippocampal volumes and true memory at Time 1, between right hippocampal volumes and false memory at Time 1, between right fusiform gyrus volume and false memory at Time 2, and between right fusiform gyrus surface area and true and false memories at Time 2) remained significant after correction for multiple testing by the Benjamini and Hochberg's false discovery rate method (Benjamini and Hochberg 1995).

To examine whether these brain regions made unique contributions to memory, linear regression analyses were conducted. We used one of the memory performance scores (i.e., short-term true memory, short-term false memory, long-term true memory, and long-term false memory, separately) as the dependent variable, and all the anatomical indices as the independent variables. Age, sex,

Table 1 Partial correlations between anatomical indices of brain regions of interest (mean ± standard deviation) and memory indices after controlling for age, sex, and intracranial volume ($N = 205$)

Brain structures	Mean ± SD of volume (*V*), surface area (SA), and thickness (*T*) for each brain region of interest	Correlations between anatomical indices and memory			
		True memory (Time 1)	False memory (Time 1)	Long-term true memory (Time 2)	Long-term false memory (Time 2)
Hippocampus	LHPV (4018.26 ± 306.33)	**0.19****	**−0.15***	0.08	−0.07
	RHPV (4149.32 ± 345.26)	**0.22**[a]	**−0.20****	0.05[a]	−0.05
Fusiform gyrus	LFGV (11,153.97 ± 1359.72)	0.02	−0.04	−0.03	0.09
	LFGSA (3521.94 ± 406.45)	0.05	−0.09	−0.01	0.06
	LFGT (2.73 ± 0.10)	−0.07	0.09	−0.02	0.11
	RFGV (10,772.55 ± 1314.96)	**−0.16***	**0.15***	**−0.17***	**0.23****
	RFGSA (3388.71 ± 385.76)	−0.13	0.12	**−0.19****	**0.21****
	RFGT (2.80 ± 0.11)	−0.04	0.05	0.04	0.07
Parahippocampal gyrus	LPHGV (2375.30 ± 345.84)	**0.14***[b]	**−0.15***[c]	−0.06[b]	0.03[c]
	LPHGSA (756.81 ± 108.81)	0.05	−0.04	−0.09	0.04
	LPHGT (2.67 ± 0.28)	**0.16***	**−0.18***[d]	0.04	0.00[d]
	RPHGV (2248.27 ± 323.28)	0.09[e]	−0.13[f]	−0.14[e]	0.10[f]
	RPHGSA (720.90 ± 101.28)	0.03[g]	−0.04	**−0.15***[g]	0.04
	RPHGT (2.71 ± 0.24)	0.08	−0.1	0.02	0.09

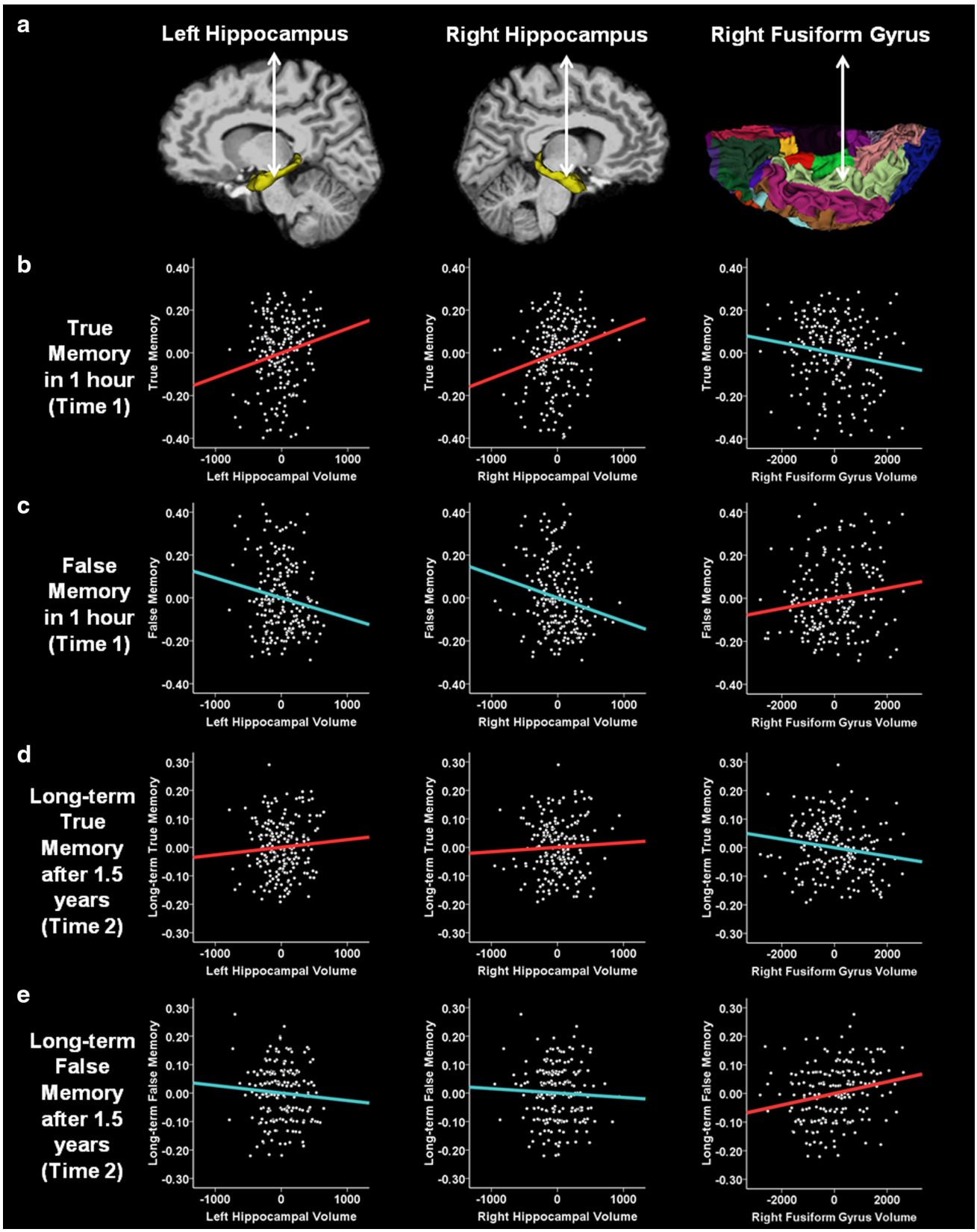
* $p < 0.05$, ** $p < 0.01$. The units of brain structural volume, surface area, and thickness are mm^3, mm^2, and mm, respectively. *HP* hippocampus, *FG* fusiform gyrus, *PHG* parahippocampal gyrus, *L* left, *R* right, *V* volume, *SA* surface area, *T* thickness. Signification correlations are shown in bold. Significant differences between correlations (tested after Fisher's r-to-z transformation) for Time 1 and Time 2 are indicated by the same superscripts. Specific statistics are as follows: [a] $Z = 1.72$, $p = 0.0427$ (one-tailed), $p = 0.0854$ (two-tailed); [b] $Z = 1.99$, $p = 0.0223$ (one-tailed), $p = 0.0466$ (two-tailed); [c] $Z = 1.80$, $p = 0.0359$ (one-tailed), $p = 0.0719$ (two-tailed); [d] $Z = 1.80$, $p = 0.0359$ (one-tailed), $p = 0.0719$ (two-tailed); [e] $Z = 2.29$, $p = 0.0110$ (one-tailed), $p = 0.0220$ (two-tailed); [f] $Z = 2.29$, $p = 0.0110$ (one-tailed), $p = 0.0220$ (two-tailed); [g] $Z = 1.80$, $p = 0.0359$ (one-tailed), $p = 0.0719$ (two-tailed)

and ICV were also included as covariates. For true memory at Time 1, two predictors were significant: right hippocampal volume [$t(187) = 3.17$, $p = 0.0018$] and right fusiform gyrus volume [$t(187) = -2.89$, $p = 0.0042$]. For false memory at Time 1, four predictors were significant: right hippocampal volume [$t(187) = -2.83$, $p = 0.0051$], right fusiform gyrus volume [$t(187) = 3.23$, $p = 0.0011$], left parahippocampal gyrus thickness [$t(187) = -2.34$, $p = 0.0201$], and left fusiform gyrus surface area [$t(187) = -2.32$, $p = 0.0204$]. For true memory at Time 2, there was no significant predictor. For false memory at Time 2, the right fusiform gyrus volume was the only significant predictor [$t(187) = 3.46$, $p = 0.0007$]. The other anatomical indices did not make unique contributions (all *p*s >0.05).

To take a closer look at the control variables of age, ICV, and gender, we correlated age and ICV with memory and anatomical variables (Table S1) and conducted ANOVAs with gender. There was no significant correlation between age and the other variables (i.e., memory and anatomical variables) ($p > 0.05$), perhaps due to the restricted age range of the college student sample. There was no significant correlation between memory indices and ICV ($p > 0.05$). ICV had positive correlations with the volumes of bilateral hippocampi, and volumes and surface areas of bilateral fusiform gyrus and parahippocampal gyrus ($p < 0.001$). However, ICV had a weak negative correlation with left parahippocampal gyrus thickness ($p < 0.05$). In terms of gender differences, ANOVAs showed that males had significant larger ICV, bilateral hippocampal volumes, bilateral fusiform gyrus and parahippocampal gyrus volumes and surface areas than did females ($p < 0.001$). There was no significant gender difference for memory indices and thickness of bilateral fusiform gyrus and parahippocampal gyrus ($p > 0.05$).

Next, to help understand the relations among the anatomical variables, we examined partial correlations between different anatomical indices after controlling for age, sex, and ICV (Table S2). Results suggested that bilateral hippocampal volumes were positively associated with bilateral parahippocampal gyrus volume and thickness ($p < 0.01$), but there was no significant correlation between bilateral hippocampal volumes and bilateral fusiform gyrus anatomical indices ($p > 0.05$), except for a small positive correlation between left hippocampal volume and right fusiform gyrus thickness.

Finally, we used Fisher's r-to-z transformation to allow for direct comparisons of the partial correlations between


a
Left Hippocampus
Right Hippocampus
Right Fusiform Gyrus
b
True Memory in 1 hour (Time 1)
True Memory
Left Hippocampal Volume
Right Hippocampal Volume
Right Fusiform Gyrus Volume
c
False Memory in 1 hour (Time 1)
False Memory
d
Long-term True Memory after 1.5 years (Time 2)
Long-term True Memory
e
Long-term False Memory after 1.5 years (Time 2)
Long-term False Memory

◀**Fig. 2** Brain regions of interest and the relationships between their volumes and memory performance at Time 1 and Time 2. **a** Freesurfer subcortical segmentation of the hippocampus and Freesurfer parcellation for a single subject. Models are displayed on one randomly chosen male subject. Left and right hippocampal 3D surface models (*yellow*) created with Slicer derived from the Freesurfer subcortical segmentations. Right fusiform gyrus (*light cyan*) created with Slicer derived from the Freesurfer parcellation results. **b–e** Partial regression plots showing the relationship between brain region volume (i.e., left hippocampal volume, right hippocampal volume, and right fusiform gyrus volume) and memory performance (i.e., true memory, false memory, long-term true memory, and long-term false memory). Variables in the partial regression plots are residuals after controlling for sex, age, and the intracranial volume. *Red regression lines* represented positive associations and *blue regression lines* represented negative associations. Hippocampal volume was associated positively with true memory and negatively with false memory at Time 1, but their associations were not significant at Time 2. In contrast, right fusiform gyrus volume was associated positively with false memory and negatively with true memory both at Time 1 and Time 2

Time 1 and Time 2. As shown in Table 1, there were four significant differences for true memory and three significant differences for false memory. True memory had higher (more positive) correlations with right hippocampal volume, left parahippocampal gyrus volume, right parahippocampal gyrus volume, and right parahippocampal gyrus surface area at Time 1 than at Time 2. False memory had lower (more negative) correlations with left parahippocampal gyrus volume, left parahippocampal gyrus thickness, and right parahippocampal gyrus volume at Time 1 than at Time 2.

Discussion

This study provides several novel insights into the neural basis of true and false memories. First, we found evidence that bilateral hippocampal volumes were associated with short-term (within 1 h) true and false memories, but not with long-term (1.5 years) true and false memories. This result is consistent with idea that the key role of the hippocampus in memory is time-limited. Second, we found evidence that right fusiform gyrus volume was associated with both short-term and long-term true and false memories, and right fusiform gyrus surface area was associated with long-term true and false memories. Moreover, both right hippocampal volume and right fusiform gyrus volume contributed to short-term true and false memories, whereas the contributions of the right fusiform gyrus volume were unique to long-term false memory. Compared with the hippocampus, the role of the right fusiform gyrus in memory was more consistent across time. To our knowledge, this is the first study showing that individual differences in true and false memories arising from misinformation are associated with measureable differences in the volumes of the hippocampus (for short-term memory), and in the volume and surface area of right fusiform gyrus (for long-term memory) in healthy young adults.

Hippocampal volumes were positively associated with true memory and negatively associated with false memory. Our results are consistent with previous studies of true memory using different memory tasks (Ashtari et al. 2011; Gur et al. 2000; Molnar and Keri 2014; Pohlack et al. 2014), and extended them to false memory, which had a highly negative correlation with true memory in the current misinformation study. For example, one of these studies asked subjects to study words form list A and then study words from list B, and finally try to recognize studied words from list A only (Pohlack et al. 2014). It was found that hippocampal volume was positively correlated with the ability to discriminate studied words from list A from lures (i.e., lures are either words from list B or unstudied words that sound alike or share the same semantic categories as the words in list A). Previous studies also suggested that true memory was related to greater hippocampal activations during a misinformation task (Baym and Gonsalves 2010; Okado and Stark 2005; Stark et al. 2010), but the direction for the correlation between hippocampal volume and hippocampal functional activation during memory tasks was inconsistent across samples of different age groups (Gimenez et al. 2005; Powell et al. 2007; Putcha et al. 2011; Sandstrom et al. 2006). Our findings were consistent with previous studies using young subjects (Gimenez et al. 2005; Powell et al. 2007), and inconsistent with previous studies using elderly subjects (Putcha et al. 2011; Sandstrom et al. 2006). Future study should directly contrast young and elderly subjects in terms of the relationships between hippocampal volume, hippocampal activation during a misinformation task, and true and false memories.

Our finding that hippocampal volume was associated with short-term but not long-term memory is in line with previous research on the neural basis of long-term memory. Experimental studies with animals have suggested that disrupting hippocampal function impairs recent memory but not remote memory (e.g., 30 days) (Frankland and Bontempi 2005). Human patients with brain damage limited to the hippocampus showed impaired episodic memories of recent events but not for memories from the remote past (e.g., years earlier) (Kirwan et al. 2008). These studies, as well as ours, support a consolidation model that posits that the hippocampus is a rapid and temporary learner (Mcclelland et al. 1995).

Among various cortical areas, we focused on the right fusiform gyrus for its essential role in specific recognition and sensitivity to minor perceptual changes (Garoff et al. 2005; Simons et al. 2003). As predicted, right fusiform

gyrus volume was correlated with short-term and long-term true and false memories, and these associations were independent of the effect of the hippocampus. The role of the fusiform gyrus in false memory is further supported by studies showing that electrical stimulation of the fusiform gyrus produced complex visual illusions like faces, animals, and images from memory in epilepsy patients (Lee et al. 2000). The cortical grey matter volume is the product of cortical surface area and cortical thickness. The right fusiform gyrus volume and surface area, but not its thickness, were correlated with long-term true and false memories. Consistent with previous findings (Winkler et al. 2010), the fusiform cortical grey matter volume was more closely related to surface area than cortical thickness. A previous study also found that fusiform gyrus volume and surface area had similarly negative correlations with phonological awareness for both dyslexic and typical adults, but its thickness was not correlated with phonological awareness for either group of subjects (Frye et al. 2010). Consistently with their findings, we found that the right fusiform gyrus volume and surface area had similar negative correlations with long-term true memory, but its thickness was not correlated with memory performance in young healthy adults. A recent study also suggested that the relationships between cognitive ability and these two cortical measures (i.e., thickness and surface area) were different for healthy subjects in the age range of 9–60 years (Schnack et al. 2015). Future study should explore the associations between all three structural indices of the fusiform gyrus (volume, surface area, and thickness) and memory performance in different samples across life span.

To interpret the differential relationships of the surface area and thickness of the right fusiform gyrus with memory performance, it is important to understand the underlying cellular and genetic mechanisms. First, based on the radial unit hypothesis, cortical surface area reflects the number of radial columns vertical to the pial surface, whereas cortical thickness reflects the horizontal layers in the cortical columns (Rakic 2009). Individual differences in surface area and in thickness are determined by the number of these columns and by the number of cells within a given column, respectively. Second, surface area changes are mainly determined during early development, whereas the thickness changes could be seen throughout the entire lifespan. Third, twin studies suggested that both surface area and thickness are heritable (e.g., with heritability of 58 % for surface area and 40 % for thickness of the fusiform gyrus), but they may be influenced by different genetic and environmental factors (Panizzon et al. 2009; Winkler et al. 2010). Importantly, a recent twin study showed that cortical surface area, rather than cortical thickness, was related phenotypically and genetically to general cognitive ability (Docherty et al. 2015). Therefore, we speculate that individual differences in the surface area of right fusiform gyrus are more likely to be influenced by genetic factors during early development, which need further research.

In addition, the memory-anatomy correlation for left parahippocampal gyrus was similar to those for the hippocampus (i.e., its anatomical volume was positively correlated with short-term true memory and negatively correlated with short-term false memory, but it was not correlated with long-term true and false memories). The association between left parahippocampal gyrus volume and true memory is consistent with previous functional results implicating left parahippocampal gyrus in recent true memory using the misinformation paradigm (Okado and Stark 2005; Stark et al. 2010). However, compared with the hippocampus and right fusiform gyrus, the role of the parahippocampal gyrus's structure in true and false memories from misinformation was relatively minor and depended on the type of memories. Based on the regression analysis, the parahippocampal gyrus's structural indices did not make unique contributions to memory performance. Based on the memory-anatomy correlation comparisons between Time 1 and Time 2, there were significant differences between Time 1 and Time 2 for the correlations between the parahippocampal gyrus and memory.

To interpret the differential relationships of the structural variations of the hippocampus and right fusiform gyrus with short- and long-term true and false memory, it is crucial to understand the different roles of the hippocampus and right fusiform gyrus in memory. According to multiple trace theory, recent memory traces in the hippocampus included spatial and temporal context, but both recent and remote memory traces in the cortical regions such as right fusiform gyrus are context-free in nature (Frankland and Bontempi 2005). To increase true memory and reduce false memory, subjects need to differentiate the post-event misinformation from the original information, which requires the rich context information integrated in the hippocampus. Consistent with the previous study (Pohlack et al. 2014), subjects with a larger hippocampus were better at discriminating memory from different sources and hence showed better short-term true memory in the current study. In contrast, post-event misinformation is likely to be stored in cortical areas such as the right fusiform gyrus, which may explain the positive correlations between short- and long-term false memory and right fusiform gyrus volume in the current study. According to the standard consolidation model of memory, the hippocampus is a fast but transient learner, while the cortex is a slow but long-lasting learner (Frankland and Bontempi 2005). Supporting this theory, we found that hippocampal volumes were related to short-term but not long-term memory, whereas the right fusiform gyrus volume was related to both short- and long-term memory.

Several limitations of the present study need to be mentioned. First, our sample included only young healthy adults, which did not allow us to examine age differences in the neural correlates of true and false memories. Future study should include both young and elderly subjects. Second, we used a relatively short event-misinformation delay (i.e., 30 min) in the current study, which may limit its practical implications. In real-life legal cases, there might be shorter or longer delay between seeing the event and receiving the misinformation for eyewitness. Future studies need to explore if the event-misinformation delay may affect the neural correlates of true and false memories.

In conclusion, individual differences in short-term true and false memories from misinformation were associated with structural variations of the hippocampus and right fusiform gyrus, whereas those in long-term true and false memories were associated with structural variations of the right fusiform gyrus.

Acknowledgments This study was supported by the National Natural Science Foundation of China (31571132), the Fundamental Research Funds for the Central Universities (2013YB27), and the 111 Project of the Ministry of Education of China (B07008). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. The authors thank Yoko Okado and Craig Stark for sharing their slides with us and for their valuable input.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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