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# Cross-cultural comparison of the neural correlates of true and false memory retrieval

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#### ABSTRACT

Prior work has shown Americans have higher levels of memory specificity than East Asians. Neuroimaging studies have not investigated mechanisms that account for cultural differences at retrieval. In this study, we use fMRI to assess whether mnemonic discrimination, distinguishing novel from previously encountered stimuli, accounts for cultural differences in memory. Fifty-five American and 55 Taiwanese young adults completed an object recognition paradigm testing discrimination of old targets, similar lures and novel foils. Mnemonic discrimination was tested by comparing discrimination of similar lures from studied targets, and results showed the relationship between activity in left fusiform gyrus and behavioural discrimination between target and lure objects differed across cultural groups. Parametric modulation analyses of activity during lure correct rejections also indicated that groups differed in left superior parietal cortex response to variations in lure similarity. Additional analyses of old vs. new activity indicated that Americans and Taiwanese differ in the neural activity supporting general object recognition in the hippocampus, left inferior frontal gyrus and middle frontal gyrus. Results are juxtaposed against comparisons of the regions activated in common across the two cultures. Overall, Americans and Taiwanese differ in the extent to which they recruit visual processing and attention modulating brain regions.

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Cross-cultural; long-term memory; fMRI; pattern separation; mnemonic discrimination; old vs. new; true vs. false memory

How culture influences one's thoughts, behaviour and brain activity is a critical area of study. Our minds are shaped by a lifetime of experiences as we navigate through physical space, engage in social interactions and solve problems. Culture can be defined in terms of shared experiences – living in a particular geographic location, adhering to a set of social norms, having common goals and priorities (Gutchess & Rajaram, 2023; Wang, 2021). Understanding how these shared experiences affect cognition is essential for developing theories of psychology and neuroscience that reflect the immense amount of diversity among human beings.

One of the most enduring approaches in the field of cross-cultural psychology involves comparing Easterners and Westerners, commonly conceptualised in terms of differing social orientations (i.e., collectivism in the East versus individualism in the West). However, recent work has also investigated cross-cultural differences through the lens of perceptual and mnemonic cognitive processes (see Gutchess & Sekuler, 2019 for an overview). Americans are more likely to recognise previously-seen items and discriminate them from similar lures than East Asians (Leger & Gutchess, 2021; Mickley Steinmetz et al., 2018; Millar et al., 2013). Although cross-cultural neuroscience has largely focused on social processes (Chiao et al., 2013; Kitayama et al., 2019; Sasaki & Kim, 2017), some neuroimaging studies have identified the hippocampus, fusiform gyrus and occipital cortex as regions exhibiting cultural differences in activity relating to viewing and forming specific memories of objects (Ksander et al., 2018; Paige et al., 2017). Other work focusing on object processing during incidental encoding found cross-cultural differences in several regions including temporal gyrus, superior parietal/angular gyrus and superior temporal/supramarginal gyrus (Gutchess et al., 2006). Another study also found cultural differences in object processing regions (i.e., lateral occipital complex, LOC) between East Asian and Western older adults (Goh et al., 2007). The existence of cross-

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cultural differences in visual object processing regions, implicated in both mnemonic and non-mnemonic analyses, suggests that culture groups differ in their mental representations of encoded objects. This corroborates prior behavioural work indicating that cross-cultural differences in object discrimination performance may be rooted in differences in the amount of perceptual detail within encoded representations (Leger & Gutchess, 2021).

One candidate explanation to account for cross-cultural differences in object memory, not yet tested neurally across cultures, is mnemonic discrimination. This process involves distinguishing novel episodes or stimuli from those encountered previously, including comparison of signals consistent with hippocampal pattern separation. Pattern separation reflects distinct "old" and "new" representations, allowing individuals to avoid false endorsements of similar objects or events (Davidson et al., 2019; Yassa & Stark, 2011). This process contrasts pattern completion, which reinstates stored representations based on partial cues. Pattern separation and pattern completion are commonly mischaracterised as being two ends of a single unitary process (i.e., more pattern separation implies less pattern completion and vice versa). However, it is more accurate to consider them as distinct processes, both of which can be elicited by novel and previouslyencountered stimuli (Hunsaker & Kesner, 2013; Pidgeon & Morcom, 2016).

Mnemonic discrimination could contribute to the specificity of memory, such that having highly distinct mental representations could better inform the discrimination of target and lure items. In a study of young Americans (mean age = 20.8), activity in DG/CA3 regions of the hippocampus was higher in response to presentations of similar lures compared to previously-studied items (Lacy et al., 2011). This heightened activity was also seen during presentation of novel items. Typically, neural activity is suppressed in response to repeated stimuli (Krekelberg et al., 2006), but the response to similar lures did not exhibit this adaptation effect. Rather, neural activity for similar lures resembled the response for novel items, leading the researchers to conclude that successful pattern separation depends upon this subfield of the hippocampus correctly processing similar lures as previouslyunseen stimuli. Although the hippocampus's contribution to pattern separation has been highly studied, there is also evidence that cortical regions, including perirhinal cortex (Kent et al., 2016; Stevenson et al., 2020) and occipital and inferior frontal cortex (Pidgeon & Morcom, 2016), also contribute to mnemonic discrimination processes. Mnemonic discrimination can vary across groups, with older adults and particularly those at risk for dementia, performing poorer on pattern separation than younger adults (Stark et al., 2013; Stark et al., 2015).

It is possible that individual differences in mnemonic discrimination could occur across other groups, including cultures. Effects of culture could indicate group differences in the proneness, or facility, of pattern separation processes. That is, mnemonic discrimination processes related to pattern separation could account for the prior findings indicating that Americans exhibited higher levels of memory for details of objects than East Asians. The present study investigates cross-cultural differences in the neural activity underlying recognition of pictures of everyday objects during retrieval, and operationalises "culture" based on the comparison of individuals born and raised in two different countries that are associated with varying traditions, languages, values and information processing styles. While in the scanner, American and Taiwanese participants made memory decisions for previously-seen old items (e.g., beverage in a curved glass with two straws; see Figure 1), similar-but-not-identical lures (e.g., beverage in a cylindrical glass with one straw), and completely new items. Pattern separation analyses focused on activity related to correctly determining that similar lures were "new" compared to mistakenly calling them "old" (i.e., correct rejections versus false alarms). That is, these analyses identified neural regions involved in correctly distinguishing new information, rather than erroneously endorsing false memories. Based on the prior pattern separation and cross-cultural memory literatures, we predicted Americans, compared to Taiwanese, would demonstrate more activity in medial temporal lobes (MTL), including hippocampus (e.g., Lacy et al., 2011) and parahippocampal gyrus (e.g., Paige et al., 2017), during correct rejection of lures compared to false alarms. Additionally, prior cross-cultural (Goh et al., 2007; Ksander et al., 2018; Paige et al., 2017) and mnemonic discrimination studies drawing on a pattern separation framework (Kent et al., 2016; Pidgeon & Morcom, 2016; Stevenson et al., 2020) implicate visual processing areas as having a role in object memory, so we also predicted the same pattern of cross-cultural neural activity



**Figure 1.** Examples of lure stimuli which share some features and a semantic label but also differ in some feature dimensions such that they can be successfully discriminated from one another. Distinguishing feature dimensions include count and orientation (number of straws in a beverage; ice cream cone tilted at an angle vs. standing straight up), color (light brown coffee versus dark brown chocolate), and state and size (curved vs. cylindrical drinking glass; arrangement of balloons; larger vs. smaller balloons). Similarity bin labels for the example images are noted.

differences for correct rejections versus false alarms would emerge in fusiform gyrus and LOC. This would suggest that differences in the reactivation of perceptual information and mnemonic discrimination processes consistent with hippocampal pattern separation contribute to cultural differences in episodic memory for perceptually-rich objects. The fusiform also has emerged in cross-cultural comparisons of memory at encoding (Paige et al., 2017), interpreted as reflecting the contributing to the formation of specific, detailed memory traces (Garoff et al., 2005; Koutstaal et al., 2001). Cultural differences in activating this region could extend to retrieval, as a function of the specificity of retrieved memories and reflecting the recapitulation of visual processes (e.g., Wheeler et al., 2000). Beyond these ROI analyses, we also conducted exploratory whole-brain analyses to investigate the possibility of crosscultural differences in regions beyond medial temporal and visual areas, such as frontal regions associated with higher-order retrieval monitoring processes (e.g., de Chastelaine et al., 2016) or parietal regions sensitive to the contents of retrieval (e.g., Wagner et al., 2005).

In addition, we sought to further contextualise comparisons of pattern completion by understanding how culture influences the neural underpinnings of old versus new recognition as well as true versus false memories. Old versus new analyses focused on correct "old" responses to studied items (i.e., hits) compared to correct "new" responses to novel items (i.e., correct rejections), whereas true versus false memory analyses focused on correct "old" responses to studied items (i.e., hits) compared to incorrect "old" responses to similar lures (i.e., false alarms). Cultures may differ in their recruitment of mnemonic processes that contribute to memory errors, as well as in the aspects of information that they prioritise and retrieve in accurate memories. These complementary analyses together contribute to a fuller understanding of the conditions under which culture can influence memory, including considering the pervasiveness of cultural influences in supporting accurate as well as erroneous memory. These additional analyses inform our interpretations of our primary mnemonic discrimination analyses by allowing us to assess whether cultural effects are specific to this process or generalise across object memory processes (e.g., discriminating similar from old items; distinguishing new from old items). We conducted these analyses in the same ROIs as the mnemonic discrimination analyses and also used exploratory whole-brain analyses.

#### Method

#### **Participants**

Fifty-five American (25 male) and 55 Taiwanese (27 male) young adults (ages 18–30) completed this study. Originally, 60 Americans and 60 Taiwanese were scanned, but two American participants and three Taiwanese were not included in the final sample due below chance performance on discriminating between old and novel items and software errors during task administration. Additionally, one American participant was dropped from analyses due to excessive motion during scanning (mean framewise displacement > 0.5 mm for all runs and more than 20% of images in each run were flagged as outliers during preprocessing pipeline), and two American and two Taiwanese participants were not included in analyses due to issues during scanning (i.e., did not complete all memory task runs, technical problems with scanner).

The sample size was selected based on a power analysis conducted for a 2 (Culture: Americans, Taiwanese) × 2 (Lure Response: correct rejection, false alarm) repeated measures ANOVA using the software G\*Power (Faul et al., 2007) and also accounting for the loss of participants from the sample due to technical errors or failure to follow task instructions. The analysis recommended samples of at least 30 participants per cultural group to detect an interaction, based on assuming a medium effect size of  $\eta p^2 = 0.12$ ,  $1-\beta = 0.8$  and alpha = 0.05. The effect size was based on prior findings of differences in hippocampal activity for viewing lures vs. previously-seen items (Bakker et al., 2008). We targeted larger sample sizes in order to have more robust and stable estimates of cultural differences.

Americans were defined as those who were born in the United States and had not lived abroad more than 5 years. Americans were recruited from Brandeis University and the surrounding Greater Boston area. Taiwanese were defined as those who were born in Taiwan and have not lived abroad more than 5 years. Taiwanese were recruited at National Taiwan University in Taipei, Taiwan. All participants completed a demographics guestionnaire which included questions about nationality, race, sex and years of education. Only young adults between the ages of 18-30 were eligible to complete the study. The American sample included the following racial backgrounds: White (n = 46), Black/African American (n = 1), American Indian/ Alaskan Native (n = 1), and multiracial (n = 7); participants of Asian ethnicity were excluded to support a clearer distinction of the American sample from the East Asian (Taiwanese) sample. Eight American participants identified as being of Hispanic ethnicity. The entire Taiwanese sample was of Asian descent. The samples had similar ages (American M = 21.27, SD = 3.26; Taiwanese M =23.20, SD = 2.47) and years of education (American M =15.31, SD = 2.23; Taiwanese M = 16.74, SD = 1.99), although the Taiwanese sample was moderately older than the American sample, t(1108) = 3.50, p < .001, Cohen's d =0.67, and also had more years of education, t(1108) =3.51, *p* < .001, Cohen's *d* = 0.78.

All study procedures, consent forms and stimuli were approved by local ethics committees in both the United States (i.e., Institutional Review Board) and Taiwan, and all participants gave written informed consent. This study was performed in line with the principles of the Declaration of Helsinki.

### Neuropsychological assessments

In a separate session prior to the scan, each participant completed a battery of neuropsychological tasks. These tasks were administered in order to demonstrate culture groups had equivalent ability across a range of cognitive domains and to ensure cognitive abilities would not be confounded with cultural factors. Tasks included the California Verbal Learning Test Second Edition (CVLT-II, Delis et al., 2000), the Corsi block-tapping test from the Wechsler Memory Scale-III (Wechsler, 1997; Chinese version: Hua et al., 2005) and the Colour Trails Test (CTT, D'Elia et al., 1996; see Lee & Chan, 2000; Zhao et al., 2013 for use in China). To further minimise cultural confounds, participants completed tasks in their native language, and tasks were chosen for their cultural fairness, informed by consultation with a Taiwanese neuropsychologist who trained in North America. For example, to measure sustained and divided attention, we used the Colour Trails Test rather than the commonly used Trail Making Test that includes English letters.

# Mnemonic similarity task

While in the scanner, participants completed the Mnemonic Similarity Task (MST), a commonly used measure reflecting the behavioural outcome of hippocampal pattern separation (Kirwan et al., 2007; Stark et al., 2015). The Python code version of the task was downloaded directly from the task developer's site (https://faculty. sites.uci.edu/starklab/mnemonic-similarity-task-mst) and was then modified for fMRI use. The task contains images of real objects (e.g., a calculator, balloons, a pair of shoes) which were presented in random order, and each item's condition at test (i.e., old, similar, or new) was randomly assigned for each participant. This randomisation was done so that task performance would not be confounded by presentation order or certain items being assigned to certain conditions.

Only a subset of images from the original stimulus set were used in order to ensure cultural fairness. All images with written words, specific cultural associations (e.g., a Halloween jack-o-lantern), or poor visual quality were removed, based on the judgments of Chinese and American lab members. The remaining items were normed, with a final total sample with usable data from 47 American and 44 Taiwanese older adults (60 years or older; we focused on older adults as part of a larger aging study). Participants rated familiarity and provided open-ended responses to name the items. Images were divided into subsets for online data collection through Qualtrics, with 5-8 participants from each cultural group responding for each item. For each item, participants rated familiarity on a 1-5 scale; for an item (or its paired similar item) to be included in the final image set, both culture groups needed to have an average rating of at least 3 out of 5, as well as average correct naming of at least 50%. Although

this method for norming stimuli yielded a more culturally fair image set compared to the original MST image set, we acknowledge the limitations of having a small sample size and lack of younger adult samples.

Each item and its similar lure had been labelled with a value 1-5 indicating the level of similarity between the two items; these values had been assigned based on item similarity experiments conducted by the original task creators (Lacy et al., 2011). Participants saw an equal number of items from each of the five similarity levels. A value of 1 indicated items that were most similar to each other and 5 indicated items that were least similar (i.e., most distinct). Because the original similarity bins were derived from an American sample, we also generated our own culturally fair similarity labels, used in analyses, based on participants who successfully completed the behavioural task from a partially-overlapping subset of our recruited sample (American n = 49, Taiwanese n = 59). Pilot data suggested that creating the bins in this way resulted in smaller, more consistent performance differences between the two cultures over the five levels of difficulty rather being exaggerated for some levels and converging for the most difficult items (a pattern also seen in Leger & Gutchess, 2021). Participants saw an equal number of items from each of the five similarity levels.

Participants completed the encoding phase of the MST in the scanner while anatomical images were being acquired. During the encoding phase, participants viewed 128 images one at a time, each shown once for 4 s. There was 800-12,000 ms of fixation jittered between trials. Fixation lengths were determined using Optseq, a software designed to optimise stimulus presentation timing according to the haemodynamic response function (Dale et al., 1999). To ensure participants' attention during this encoding phase, they were asked to indicate with a button box whether the current object on the screen belonged indoors or outdoors. Upon completion of this task participants viewed a fixation cross for a 7 min resting-state scan,<sup>1</sup> and then completed a surprise recognition test, which is the focus of these analyses. In this test phase, they were shown some of the same images from the encoding phase as well as images that were similar (see Figure 1 for examples) and images that were completely novel. For each participant, half of the 128 object they viewed during encoding were assigned to the Old condition (the exact image was presented again at test) while the other half were assigned to the Similar condition (a similar-but-not-identical image was presented at test). Sixty-four images of each test condition (i.e., Old, Similar and New) were presented in a randomised order of 192 total trials. Images appeared on screen for 4 s followed by fixation. Participants indicated using buttons whether the image was "old" (seen before during encoding) or "new" (same semantic label but not identical to the image seen during encoding or a completely novel item). Finally, participants completed an unrelated lottery value-based decision making task.<sup>2</sup>

### Neuroimaging data acquisition and processing

#### Data acquisition

Imaging data in the United States was collected at the Harvard Center for Brain Science, Cambridge MA. Imaging data in Taiwan was collected at the Imaging Center for Integrated Body, Mind and Culture Research, National Taiwan University, Taipei. Both sites used 3.0 T Siemens MAGNETOM Prisma whole-body MRI systems (Siemens Healthcare, Erlangen, Germany).

Prior to beginning data collection, calibration analyses were conducted on the same participants tested across sites to ensure comparability of scanners. Global signal did not meaningfully differ across scanners and activation differences across sites were limited to primary visual cortex, likely caused by differences in task screen luminance (Chen et al., 2020; see also Lee et al., 2021 for a comparison of cultural groups using these scanners). These calibration results align with prior work indicating that site minimally accounts for group differences and that between-subject variance can be much larger than between-site variance (Sutton et al., 2008).

Images were acquired using a 64-channel head coil (Siemens Healthcare). Functional images were acquired with a simultaneous multi-slice echo-planar image (EPI) sequence (Moeller et al., 2010; Setsompop et al., 2012; Xu et al., 2013), obtaining 65 slices 2.3 mm thick (TR = 800 ms, TE = 25 ms, FOV = 220 mm, flip angle = 60°, SMS factor = 5, in-plane acceleration = 2). The SMS-EPI acquisition used the CMRR-MB pulse sequence from the University of Minnesota. A high resolution T1-weighted, magnetisation-prepared rapid gradient echo image (multi-echo MPRAGE: Van der Kouwe et al., 2008) was acquired with 176 sagittal slices, voxel size  $1.0 \times 1.0 \times 1.0 \text{ mm}$ , FOV = 256 × 256 mm, TR = 2530.0 ms, short TE = 1.69 ms, long TE = 7.27 ms and FA = 7°.

### Preprocessing

Preprocessing was performed using fMRIPrep 20.0.6 (Esteban et al., 2019), which is based on Nipype 1.4.2 (Gorgolewski et al., 2011). For each of the functional runs, the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of fMRIPrep. A B0-nonuniformity map (or fieldmap) was estimated based on a phasedifference map calculated with a dual-echo GRE (gradient-recall echo) sequence, processed with a custom workflow of SDCFlows inspired by the epidewarp.fsl script and further improvements in HCP Pipelines (Glasser et al., 2013). The fieldmap was then co-registered to the target EPI (echo-planar imaging) reference run and converted to a displacements field map (amenable to registration tools such as ANTs) with FSL\u2019s fugue and other SDCflows tools. Based on the estimated susceptibility distortion, a corrected EPI (echo-planar imaging) reference was calculated for a more accurate co-registration with the anatomical reference. The BOLD reference

was then co-registered to the T1w reference using flirt (FSL 5.0.9; Jenkinson & Smith, 2001) with the boundary-based registration (Greve & Fischl, 2009) cost-function. Co-registration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL 5.0.9; Jenkinson et al., 2002). BOLD runs were slice-time corrected using 3dTshift from AFNI 20160207 (Cox & Hyde, 1997). The BOLD time-series were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions.

Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al., 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (CompCor, Behzadi et al., 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 5% variable voxels within a mask covering the subcortical regions. This subcortical mask is obtained by heavily eroding the brain mask, which ensures it does not include cortical GM regions. For aCompCor, components are calculated within the intersection of the aforementioned mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run (using the inverse BOLD-to-T1w transformation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components\u2019 time series are sufficient to explain 50% of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and guadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers.

Given the nature of our two distinct samples and crosscultural hypotheses, it was necessary to use a template that was representative for our sample. We used Diffeomorphic Anatomical Registration Through Exponentiated Lie algebra (DARTEL) (Ashburner, 2007) to create a culturefair anatomical template using the same sample of participants included in analyses (55 Americans, 55 Taiwanese). After preprocessing in fMRIPrep, functional images were normalised to MNI space via this DARTEL template.

#### General linear model

A first-level model was constructed with regressors for target hits ("old"|Target), lure correct rejection ("new"| Lure), lure false alarms ("old"|Lure), and foil correct rejections ("new"|Foil). Target misses ("new"|Target) and foil false alarms ("old" |Foil) were collapsed into a single regressor of noninterest given the rarity of these instances. Culturally fair lure similarity labels were also included as a parametric modulator for lure correct rejections and false alarms. Each trial was modelled by a delta function (duration = 0) defined by stimulus onset and convolved with the canonical haemodynamic response function to create regressors. See Supplementary Materials for the average number of trials going into each regressor (i.e., bin sizes) and average response times for the behavioural regressors in the first-level model. Regressors for six motion vectors (x, y, z, pitch, roll, yaw) and a framewise displacement vector derived from preprocessing were included, and we also included the five largest-value anatomical CompCor components that were derived from preprocessing. CompCor is a principal component analysis method of extracting physiological noise (Behzadi et al., 2007).

To address our hypothesis regarding cross-cultural differences in brain activity related to ability to discriminate between previously-seen and similar items (mnemonic discrimination), we created the following interaction contrasts: [Americans > Taiwanese for (Lure Correct Rejections > Lure False Alarms)], [Taiwanese > Americans for (Lure Correct Rejections > Lure False Alarms)]. Additionally, we created an interaction contrast to test effects of culture on old-new discrimination activity: [Americans > Taiwanese for (Target Hits > Foil Correct Rejections)], [Taiwanese > Americans for (Target Hits > Foil Correct Rejections)]. Also, in order to test culture effects for activity related to true recognition versus false alarms for lures, we created the following interaction contrast: [Americans > Taiwanese for (Target Hits > Lure False Alarms)], [Taiwanese > Americans for (Target Hits > Lure False Alarms)]. Parametric modulation analyses testing culture effects in response to varying lure similarity were conducted using the following contrasts: [Americans > Taiwanese for Lure Correct Rejections Parametric Modulator], [Taiwanese > Americans for Lure Correct Rejections Parametric Modulator], [Americans > Taiwanese for Lure False Alarms Parametric Modulator], [Taiwanese > American for Lure False Alarms Parametric Modulator]. All fMRI analyses were conducted using SPM12 (Wellcome Department of Cognition Neurology, London, UK).

Whole-brain analysis results were thresholded at p < .001 with an extent threshold of k = 100 voxels. Interaction contrasts and parametric modulation contrasts

were subjected to the same thresholding. This threshold was selected based on AFNI 3dClustSim algorithm to achieve a corrected alpha = 0.05 (Cox et al., 2017a, 2017b). For cross-cultural conjunction analyses, we achieved this corrected threshold by first generating a contrast thresholded at p < .01 in one cultural group and then applying a binary mask of those results to the second culture group at p < .01 for an overall p < .001, while also applying an extent threshold of k = 100 voxels. Small volume corrected ROI analyses were not subjected to the extent threshold k = 100.

Masks were generated for clusters that emerged as significant in analyses, and parameter estimates were extracted from these clusters for ad hoc analyses to determine the pattern underlying the significant interaction. Parameter estimates extracted from the interaction contrasts were correlated with behavioural discriminability, and these correlations were compared across cultures by transforming to z scores.

#### **ROI** selection

We predicted that cross-cultural memory specificity differences would manifest in medial temporal lobe (MTL) regions supporting memory as well as regions in visual cortex that contribute to rich perceptual detail of memories. For visual regions, we selected fusiform gyrus and lateral occipital complex (LOC) as regions of interest because these areas have been implicated in previous cross-cultural neuroimaging studies of memory (Goh et al., 2007; Paige et al., 2017). An MTL mask comprised of hippocampus and parahippocampal gyrus was generated using the Wake Forest University (WFU) PickAtlas toolbox for SPM12. A bilateral mask for fusiform gyrus was also generated in this manner. To create a bilateral mask for LOC, we took the conservative approach described in Cowell et al. (2017) and defined a 7 mm radius ROI centred on the mean MNI coordinates of left [-45 -70 -11] and right [42 -67 -11] LOC as reported in seven studies (Epstein et al., 2006; Grill-Spector, 2003; Grill-Spector et al., 1998; Large et al., 2005; Lerner et al., 2001; Song & Jiang, 2006; Xu, 2009).

#### Results

# Performance on neuropsychological assessment tasks

To ensure our culture group samples were matched in terms of cognitive ability, we compared performance on measures from the neuropsychological battery: CVLT2 Long Delay Free Recall and Long Delay Recognition (long-term memory) (see Chang et al., 2010 for prior use of a version of the CVLT in Taiwan), Corsi block forward and backward spatial span (visuospatial working memory capacity), and Colour Trails section times and interference score (attention allocation). Scores and results of independent samples *t*-tests for these measures are shown in

 Table 1. Neuropsychological measures compared across cultures.

	Ame	rican	Taiwa	anese		
Measure	М	SD	М	SD	t	р
CVLT2						
Long delay free recall	14.27	1.80	14.09	2.22	0.46	.65
Long delay recognition	15.60	0.76	15.47	1.01	0.75	.46
Spatial span						
Forward	9.57	1.63	10.53	1.90	2.78	** .006
Backward	8.98	1.60	9.57	1.54	1.93	.06
Colour trails						
Part 1 time (sec)	31.61	12.16	31.42	12.46	0.08	.94
Part 2 time (sec)	60.19	15.67	59.87	14.01	0.11	.91
Interference score	-1.02	.48	-1.07	0.67	0.42	.68

\*\**p* < .01.

Table 1. The samples were well-matched, with the only significant group difference occurring on the forward section of the Corsi block-tapping test. Although this task may be the most prone to administration differences across sites, rather than reflecting a true difference in ability across samples, we included Corsi spatial span as a covariate in follow-up analyses.

# Behavioural memory performance: signal detection analyses

Signal detection analyses were conducted according to the methods described by Stark et al. (2015) in which three different d' types were calculated. The d' score was our primary metric for behavioural memory performance as it measures discriminability between different item types and accounts for response bias. In measuring Target-Foil d', "old" Target responses were counted as hits while "old" Foil responses were considered false alarms, measuring ability to discriminate Target from Foil items. Lure-Foil d' measures ability to discriminate between Lure and Foil items, counting "old"|Lure as hits and "old"|Foil as false alarms. Though the hits in the Lure-Foil d' measure are not actually the correct response, the use of the "old" response on Lure items indicates influence from the relatedness of the items to previously studied ones (e.g., a d' score of 0 would suggest that the similar and new items were considered equally "new" by participants). The Target-Lure d' ("old"|Target = hit, "old"| Lure = false alarm) was the d' type of most relevance to the question of mnemonic discrimination, as it directly measures the ability to discriminate between Old and Similar items. For all signal detection measures, sensitivity d' was calculated as z(False Alarms) - z(Hits), and response criterion c was calculated by averaging the z(Hits) and z(False Alarms) and then multiplying the result by negative one (Stanislaw & Todorov, 1999). Rates of 1 were adjusted to  $(N_{trials}-1)/N_{trials}$  and rates of 0 were adjusted to  $1/N_{trials}$ for all signal detection measures reported in this study.

A 2 (culture: American, Taiwanese)  $\times$  3 (*d*' type: Target-Foil, Lure-Foil, Target-Lure) ANOVA did not reveal a significant main effect of culture, *F*(1, 108) = 2.79, *p* = 0.10, np<sup>2</sup> =

Table 2. MST signal detection	measures across culture groups.
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	Ame	rican	Taiwanese	
Measure	М	SD	М	SD
Sensitivity ( <i>d'</i> )				
Target-foil	2.73	0.82	2.49	0.67
Lure-foil	1.58	0.67	1.53	0.45
Target-lure	1.15	0.48	0.96	0.47
Response bias (c)				
Target-foil	.24	0.31	0.25	0.31
Lure-foil	0.82	0.35	0.73	0.35
Target-lure	-0.55	0.30	-0.52	0.34

0.03, nor a significant interaction between culture and d' type, F(2, 108) = 1.60, p = 0.21,  $\eta p^2 = 0.02$ . There was a significant main effect of d' type, F(1, 108) = 374.79, p < .001,  $\eta p^2 = 0.78$ , in which performance across groups on the Target-Foil discrimination was higher than both Lure-Foil, t(109) = 22.81, p < .001, Cohen's d = 2.18, and Target-Lure, t(109) = 28.93, p < .001, Cohen's d = 2.73. d' scores for each discrimination type are shown in Table 2.

For each d' type, we also calculated associated cresponse bias measures. This measure assesses differences in the tendency to respond "old" or "new", with positive values indicating a response bias towards responding "new" (reflecting a more conservative bias in the case of remembering) and negative values indicating a bias towards "old" (reflecting a more liberal bias). A 2 (culture: American, Taiwanese) × 3 (c type: Target-Foil, Lure-Foil, Target-Lure) ANOVA revealed no main effect of culture, F (108) = 0.16, p = 0.69,  $\eta p^2 = 0.001$ , nor an interaction between c type and culture, F(108) = 2.24, p = 0.11,  $\eta p^2 =$ 0.02. There was a significant main effect of response type, F(108) = 1032.20, p < .001,  $\eta p^2 = 0.91$ . Across cultures, Target-Lure c was significantly lower (i.e., more liberal usage of "old" response) compared to Lure-Foil c, t(109) = 36.66, p < .001, Cohen's d = 3.50, and Target-Foil *c*, *t*(109) = 28.65, *p* < .001, Cohen's *d* = 2.73. Response bias measure averages for each culture group are displayed in Table 2. See Supplementary Materials for proportion correct results and behavioural analyses with Corsi spatial span included as a covariate.

# **Functional MRI**

# Mnemonic discrimination (including testing for neural correlates of hippocampal pattern separation): correct rejection vs. false alarms to similar lures

In order to investigate neural activity related to mnemonic discrimination, we conducted ROI and whole-brain analyses using the interaction contrast [Americans > Taiwanese for (Lure CR > Lure FA)], [Taiwanese > Americans for (Lure CR > Lure FA)]. There were no significant differences between cultures in our chosen ROIs (MTL, fusiform gyrus and LOC), nor did differences emerge when conducting whole-brain analyses at the cluster threshold which yields a corrected p < .05 (k = 100). Contrast results did not meaningfully change when Corsi blocks spatial span

 Table 3. Regions emerging in lure CR vs. Lure FA cultural conjunction analysis.

Region	k	Peak MNI coordinate	Brodmann areas
L parahippocampal gyrus	8	-37, -28, -21	36
R hippocampus	11	21, -5, -16	N/A
L fusiform gyrus	220	-39, -60, -7	37
R fusiform gyrus	526	32, -69, -9	19, 37
L precentral/middle frontal gyrus	272	-48, 5, 30	6, 44
R precentral/middle frontal gyrus	232	44, 16, 28	9, 44
R V2	109	32, -69, -9	18, 19

(the only neuropsychological measure which had a significant group difference) was included as a covariate in the second-level interaction contrast model.

In terms of commonalities across the cultural groups, tested with conjunction analyses, several regions emerged as significant within the MTL ROI as well as within occipital and frontal brain areas. Significant regions are displayed in Table 3 and projected onto an MNI (Montreal Neurological Institute) template image in Figure 4.

To assess cultural differences in the relationship between mnemonic discrimination brain activity and associated behavioural performance, we correlated Target-Lure d' with beta estimate differences between Lure CRs and Lure FAs for clusters in bilateral fusiform gyri, left parahippocampal gyrus and right hippocampus. These clusters emerged as significant in the cultural conjunction analyses and were selected as ROIs a priori because these areas were implicated in prior mnemonic discrimination and cross-cultural object memory studies (Goh et al., 2007; Paige et al., 2017). There was a significant difference between groups such that for right fusiform gyrus, Americans had a positive correlation between brain activity and Target-Lure discriminability, whereas for Taiwanese this association was negative. See Table 4 for correlation results.

# Effects of lure similarity: parametric modulation analyses

In addition to mnemonic discrimination activity, we were also interested in how neural activity for lure correct rejections changes as a function of lure similarity and whether this slope differed across cultures. A whole-brain cultural contrast of the similarity parametric modulator for lure CRs showed cultural differences in the left superior parietal

**Table 4.** Mnemonic discrimination activity and target-lure *d*' correlation coefficients, *z*-scores, and *p*-values.

	Amer	American		Taiwanese		Culture Comparison	
Region	r	р	r	р	Z	р	
L Fusiform	.20	.14	13	.36	1.70	.09	
L Parahippocampus	.07	.63	23	.09	1.55	.12	
R Fusiform	.24	.08	19	.16	2.23	*.03	
R Hippocampus	16	.24	.08	.56	1.23	.22	

\* *p* < .05.

lobule (k = 115; MNI coordinates: -23 -53 57; Brodmann area 7). For Taiwanese, activity in this cluster decreased as lure dissimilarity increased. For Americans, activity slightly increased as lures became more dissimilar. Results are projected onto an MNI template brain and plotted in Figure 2(a). We also conducted a small-volume corrected analysis of this same contrast using a mask of regions that emerged as significant in the mnemonic discrimination conjunction analyses, and no clusters emerged as having significant cultural differences in activity related to similarity modulation.

We also assessed how lure similarity influenced neural activity during false alarms to lures. A small-volume corrected analysis of our MTL ROI showed cultural differences in lure FA similarity parametric modulator values within left hippocampus (k = 27; MNI coordinates: -28 -25 -12). For Americans, lure FA activity in this cluster decreased as lures became more dissimilar. The opposite pattern occurred in Taiwanese; lure FA activity slightly increased in response to more dissimilar lures. Results are projected onto an MNI template brain and plotted in Figure 2(b). No significant clusters emerged as significant in a whole-brain analysis thresholded at  $k \ge 100$ , nor did any significant clusters emerge in analyses of fusiform and LOC.

In order to test for areas of similarity-modulated activity common to both Americans and Taiwanese, we also conducted lure similarity parametric modulation analyses collapsing across culture groups for both the positive and negative modulator (i.e., activity increasing/decreasing in response to more distinct lures). Significant regions for both lure CR and FA analyses are displayed in Table 5. Note that no significant clusters emerged for the lure CR positive modulator.

# Old/new memory: hits to old items versus correct rejections to new items

In addition to our primary mnemonic discrimination analyses, we analysed brain activity for old target hits versus correct rejection of new foils. By analysing cultural effects on the recognition of old objects against completely novel objects, we can determine the extent to which culture impacts more general object memory differences, compared to specific processes such as mnemonic discrimination or true/false memory, and investigate the effects of culture on multiple memory processes (e.g., retrieving accurate memories, as opposed to rejecting or mistakenly endorsing similar information in memory). We conducted ROI and whole-brain analyses using the interaction contrast [Americans > Taiwanese for (Target Hits > Foils CR)], [Taiwanese > Americans for (Target Hits > Foil CR)]. Of our chosen ROIs, only the MTL showed activation differences, with a significant cluster emerging within the right hippocampus. For this cluster, the difference between Old and New was larger for Americans compared to Taiwanese (see Figure 3(a)).





Lure FA Similarity Modulation

L Hippocampus



**Figure 2.** Results for analyses of lure similarity parametric modulator for lure correct rejections and false alarms. Cultural contrast analyses of lure CRs reveal a cluster in left superior parietal lobule emerged as having significant activity differences across cultures (A, left). Analyses of lure FAs reveal significant cultural differences in left hippocampal activity (B, left). See text for explanation of thresholds for significance. Positive betas indicate that the region responded more as image distinctiveness increased whereas negative betas indicate a stronger response as images were more similar. Beta values for the parametric modulator are plotted with individual subject points displayed (A and B, right). Error bars represent standard error of the mean between subjects.

Analyses of the whole-brain contrast revealed cultural differences in three significant clusters. The first cluster spanned across the orbital and triangular parts of the left inferior frontal gyrus. The second cluster had peak activity in the opercular part of the left inferior frontal gyrus. The third cluster spanned the left middle frontal gyrus. These regions and associated beta value plots are displayed in Figure 3(b–d). Cluster sizes and MNI coordinates for all regions emerging as significant in the interaction contrast are displayed in Table 6A. See Supplementary Materials for correlations between old vs. new activity in these regions and Target-Foil *d*'.

In addition to determining differences in neural activity related to old object recognition, we were also interested in regions in which cultural groups overlapped. Conjunction whole-brain analyses revealed that, for both cultures, the regions within parietal, prefrontal, and occipital cortices showed greater activity when recognising old objects compared to rejecting new objects. Regions are displayed in Table 6B and projected onto an MNI template brain in Figure 4. Small-volume corrected conjunction analyses for our ROIs (MTL, fusiform and LOC), selected for the mnemonic discrimination analyses, did not reveal any significant activity overlap in these regions between cultures.

Table 5. Lure similarity	parametric m	nodulation co	ollapsed	across	cultures
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		Peak MNI	Brodmann
Region	k	coordinate	areas
Lure correct rejection			
Negative modulation			
R V2	219	16, —99, 18	18
R Fusiform	151	30, -44, -9	37
Lure false alarm			
Positive modulation			
R Angular/middle temporal	215	41, -51, 25	39
gyrus			
Negative modulation			
L Middle frontal/precentral	281	-41, 25, 23	44, 46
gyrus			
R Precentral gyrus	164	41, 7, 28	6, 44
L Fusiform	160	-28, -46, -16	37
R Fusiform	447	28, -51, -16	37
L V2	234	-32, -81, 21	18, 19
R V2	231	34, -87, 9	18, 19
L Supplementary motor	142	—7, 14, 51	6
cortex			
R Posterior orbital gyrus	124	23, 32, -12	47
R Superior parietal lobule	153	25, —55, 44	7

# *True/false memory: recognition of old objects vs. False memories for similar lures*

We were also interested in how true recognition of old objects vs. false memories of similar lures was represented in the brain for each culture group. These analyses reveal the neural activity underlying successful recognition of previously-studied objects, above and beyond any familiarity signals that would also be elicited by similar lures, or, conversely, the unique activity associated with mistakenly claiming to recognise lures. We conducted ROI and whole-brain analyses using the interaction contrast [Americans > Taiwanese for (Target Hits > Lure FA)], [Taiwanese > Americans for (Target Hits > Lure FA)], and no significant regions emerged. Testing for commonalities across the cultural groups, conjunction analyses of the Target Hits > Lure FA contrast revealed that both culture groups engaged occipital, parietal and prefrontal areas. We also performed conjunction analyses focused on regions exhibiting more activity for false memories (i.e., Lure FA > Target Hits). Several frontal regions emerged significant across cultures. Table 7 displays cultural conjunction results for both contrasts, and regions are projected onto an MNI template brain in Figure 4.

#### Discussion

The present study investigated the neural mechanisms underlying cross-cultural differences in episodic memory specificity for objects. We analysed behavioural and functional neuroimaging data from American and Taiwanese participants while they completed a memory recognition task in the scanner. Based on prior object recognition and cross-cultural memory research, we hypothesised that Americans would exhibit higher levels of mnemonic discrimination activity, consistent with hippocampal pattern separation, in MTL and visual object processing regions (i.e., fusiform gyrus and LOC) compared to Taiwanese. We tested this hypothesis using a univariate interaction contrast which compared Lure CR > Lure FA activity between Americans and Taiwanese. This analysis did not reveal any regions with significant cultural difference in mnemonic discrimination activity. However, a single univariate comparison does not sufficiently account for all possible ways cultural influences on mnemonic discrimination could manifest. To assess cultural differences in the extent mnemonic discrimination activity contributes to behavioural discriminability, we correlated lure correct rejection and false alarm activation differences in ROIs with Target-Lure d'. These results were in line with our hypothesis; we observed a cultural difference in the relationship between behavioural discriminability and mnemonic discrimination activity in right fusiform gyrus. We also sought to determine how neural activity changed in response to different levels of lure similarity and whether this was affected by culture. Parametric modulation analyses of lure correct rejections indicated that groups differed in left superior parietal lobule response to variations in lure similarity, and analyses of false alarms showed differences in left hippocampus. In order to contextualise mnemonic discrimination results, we also conducted exploratory analyses for old vs. new and true vs. false neural activity, in order to assess the effects of culture across a range of retrieval processes and to test the selectivity of cultural differences to particular mnemonic processes. In addition to investigating neural differences between groups, we also tested the cross-cultural conjunctions, and across domains (mnemonic discrimination, old vs. new, true vs. false), multiple regions within occipital and frontal areas of the brain showed shared patterns of activity across culture groups. Taken together, our results provide evidence for cross-cultural differences in the neural correlates of episodic memory for objects - specifically in fusiform gyrus, parietal cortex, hippocampus and frontal gyri – and highlight patterns of functional activity that are shared across cultures.

Although no clusters emerged as significant in univariate contrast analyses of mnemonic discrimination, the correlation between mnemonic discrimination activity in the fusiform gyrus and behavioural Target-Lure discrimination differed between Americans and Taiwanese. Specifically, Americans showed a positive correlation between mnemonic discrimination activity in right fusiform gyrus and Target-Lure d' whereas for Taiwanese this relationship was negative. Right fusiform is associated with highly specific memories of visual details (Garoff et al., 2005; Koutstaal et al., 2001). Americans may be using specific feature information from right fusiform to distinguish between old and similar items, which would align with prior behavioural work indicating culture groups differ in richness of remembered details (Leger & Gutchess, 2021). The pattern for the Taiwanese, of having a negative relationship between right fusiform activity and behavioural discriminability, may indicate that rather than attending to features that distinguish similar from old items, they are



Figure 3. Results for Old/New memory: "old" [Target > "new" [Foil contrast comparing cultural groups. Clusters in right hippocampus (A, top left brain image), the opercular part of the left inferior frontal gyrus (LIFG) (B, middle brain image), the triangular and orbital parts of the left inferior frontal gyrus (C, middle brain image) and left middle frontal gyrus (D, right brain image) emerged has having significant cross-cultural differences in activity for correct recognition of old items compared to correct rejection of new items. See text for explanation of thresholds for significance. Beta values for correct responses to Target and Foil items are plotted for each region. Error bars represent between subject standard error of the mean, and individual subject data points are displayed.

Table 6. Regions emerging for the comparison of target hit vs. Foil CR (old vs. new), in terms of A: interactions with culture and B: conjunctions (common activations) across cultures.

Region	k	Peak MNI coordinate	Brodmann areas
A. Cultural interaction: target hit vs. foil CR (old	vs. new)		
R hippocampus	9	21, -7, -21	N/A
Orbital/triangular left inferior frontal gyrus	561	-44, 25, -2	45, 47
Opercular left inferior frontal gyrus	105	-48, 14, 23	44
L middle frontal gyrus	103	-25, 14, 44	6, 8
B. Cultural conjunction: target hit vs. foil CR (old	vs. new)		
L parietal cortex	1503	-32, -58, 44	7, 39
		-41, -53, 46	
		-48, -53, 51	
R parietal cortex	3735	32, -69, 48	7, 39
		41, -48, 48	
		46, -41, 48	
L dorsolateral prefrontal cortex	127	-39, 46, 2	10, 46
R dorsolateral prefrontal cortex	103	48, 41, 18	10, 46
R middle temporal gyrus	146	60, -28, -16	21
L V2	400	-7, -97, 7	18
Posterior cingulate	123	-5, -32, 28	23



Figure 4. Regions showing cross-cultural overlap in neural activity for contrasts of interest. Americans and Taiwanese engaged many of the same regions across different functional contrasts. See text for explanation of thresholds for significance.

instead attuned to features that are shared by items. In this case, reduction of right fusiform activity would be critical for avoiding false alarms.

Parametric modulation analyses of lure correct rejection activity shed further light on neural mechanisms underlying memory specificity differences. For both cultures, left superior parietal lobule activity during lure correct rejection changed depending upon how distinct lures were to their studied counterparts. For Taiwanese, left superior parietal activity increased as lure similarity increased. The pattern was opposite in Americans and also of a lower magnitude; left superior parietal lobule activity slightly decreased as lure similarity increased. Posterior parietal cortex has been implicated in supporting retrieval processes, mainly for its involvement in topdown modulation of perceptual attention (for review see: Sestieri et al., 2017). Specifically, superior parietal lobule shows increased activation in response to perceptual

Table 7. Regions emerging in target hits vs. lure FA cultural conjunction analysis.

Region	k	Peak MNI coordinate	Brodmann areas
Target hits > lure FA			
L V2	218	-7, -97, 14	18
R angular gyrus	176	51, -51, 30	39
Bilateral precuneus	332	9, -60, 28	31
Bilateral ventromedial prefrontal cortex	124	-12, 62, 2	10
Lure FA > target hits			
R precentral/middle frontal gyrus	443	48, 9, 25	6, 8, 44
L precentral/middle frontal gyrus	222	-41, 5, 28	6, 8
L insula	114	-28, 21, -2	13
R insula	159	30, 23, 0	13
Bilateral medial superior frontal gyrus	469	-7, 14, 53	6, 8

search (Sestieri et al., 2010), and retrieval goals can guide this top-down attentional process (Cabeza et al., 2008; Cabeza et al., 2011). When lures are more similar to studied items – and therefore require more effortful search for discriminating features – Taiwanese may be recruiting attentional modulation processes in the superior parietal lobule more so than Americans.

There was also evidence of cultural difference in neural response to changing similarity during lure false alarms. False alarm activity in left hippocampus increased in response to more similar lures for Americans whereas for Taiwanese, activity in this region slightly decreased. In the context of a false alarm response, Americans' decreased left hippocampal activity in response to greater lure distinctiveness aligns with our old/new contrast findings which show increased right hippocampal activity in response to correct rejection of completely novel objects. For Taiwanese, hippocampal false alarm activity increased slightly in response to more distinct lures, potentially indicating that inappropriate hippocampal pattern completion (Rolls, 2013) in response to new items is underlying false memories. The cultural divergence in false alarm activity modulation suggests that groups differ in hippocampal activity for familiarity/novelty as well as the extent to which signals consistent with hippocampal pattern separation and pattern completion inform endorsements of similar lures. Previous work has shown that neural activity during object presentation depends on the prompted memory state (e.g., encoding the object or retrieving a similar object from memory) (Long & Kuhl, 2021). During lure presentations, cultures may differ in how different levels of lure similarity/distinctiveness prompt shifts into different states such as those consistent with pattern separation/completion such that Americans are more likely to pattern separate in response to novel items whereas Taiwanese are more likely to attempt pattern completion in response to a new stimulus.

Old/new cultural contrast results also indicate differences in top-down, cognitive control processes supporting accurate object memory. American participants showed greater Target Hit vs. Foil CR activity differences in left middle frontal gyrus and the triangular/orbital parts of the left inferior frontal gyrus, which are respectively implicated in regulating visual attention (Corbetta & Shulman, 2002; Fox et al., 2006; Germann & Petrides, 2020) and controlled retrieval and selection between competing alternatives (Snyder et al., 2011). Notably, the activation values for these regions in the present study are negative relative to baseline. Although this is not a typical pattern of activity for these frontal regions, this pattern may reflect the high level of engagement of these regions throughout the retrieval task, including baseline, due to the amount of interference from highly similar items. In addition, prior work has shown reversals in activity at retrieval vs. encoding in regions comprising the default mode network (Daselaar et al., 2009), suggesting that default processes are suppressed to allow for successful encoding, possibly by reallocating neural resources to bottom-up attentional processes. In terms of the present data, Americans show greater frontal deactivation for old items compared to new items whereas for Taiwanese, deactivations did not differ between conditions. Taiwanese may be suppressing activity to increase bottom-up attentional processes during both old object recognition and new object correct rejection, whereas Americans do not reallocate resources to the same extent during correct rejections, perhaps reflecting the use of a less effortful novelty detection strategy. Cultural differences for old vs. new activity also appeared in the opercular part of left inferior frontal gyrus. Ventrolateral prefrontal cortex, which contains inferior frontal gyrus, plays a role in retrieval control processes (Badre & Wagner, 2005). The opercular part of left inferior frontal gyrus specifically has been implicated in integration of concrete contextual information in support of action planning (Badre, 2008; Badre & D'Esposito, 2007). Taiwanese may be engaging in higher-order perceptual integration processes to a greater extent than Americans when correctly remembering old objects. It is notable that our results show differing patterns of activity between subsections of ventrolateral prefrontal cortex, and there is evidence for functional seqmentation within this region (Badre, 2008; Badre & D'Esposito, 2007; Badre & Wagner, 2007). Future studies could further examine the extent to which functional differences within ventrolateral prefrontal cortex align with assumptions about culturally-influenced cognitive styles (e.g., Easterners engaging areas involving in contextual integration more than Westerners).

Beyond frontal activity differences, Americans and Taiwanese also showed differences in old vs. new activity within the right hippocampus. For Americans, right hippocampus activity was greater for correct rejection of new objects compared to recognition of old objects, but for Taiwanese, activity did not differ between conditions. Americans, more than Taiwanese, may be engaging the hippocampus in service of novelty detection (Fredes & Shigemoto, 2021; Gómez-Ocádiz et al., 2022; Knight, 1996; Kumaran & Maguire, 2009) to correctly reject novel objects. Alongside our results showing Americans have less frontal deactivation in response to novel objects compared to Taiwanese, the hippocampal findings suggest cultural differences in the neural resources recruited when processing novel stimulus information.

To aid in the interpretation of cultural differences, we tested for common activations across Americans and Taiwanese. We identified several areas of overlapping activity in brain regions which have appeared consistently in retrieval literature. In terms of mnemonic discrimination activity, cultural conjunction occurred in: right hippocampus, left parahippocampus, bilateral fusiform gyrus, right V2, and bilateral middle/precentral frontal gyrus. These cross-cultural results align with broader mnemonic discrimination and literature consistent with pattern separation which implicates hippocampus (Yassa & Stark, 2011) and occipital cortex – including fusiform gyrus (Pidgeon & Morcom, 2016). A recent theory suggests mnemonic discrimination and activity consistent with pattern separation processes could occur throughout visual cortex, depending upon the complexity of representations required for discrimination (Kent et al., 2016). Future cross-cultural work could test mnemonic discrimination activity across different types of visual stimuli (e.g., abstract stimuli, concrete objects, scenes) to investigate whether cultural effects manifest uniformly across different levels of visual complexity (see Leger et al., 2023 for one example). Parametric modulation results collapsing across groups also indicate both Americans and Taiwanese engage visual processing regions - specifically, right fusiform and right V2 the most when processing highly similar objects. Cultural conjunction results for all tested memory domains (mnemonic discrimination, old vs. new, true vs. false) indicated that both cultural groups recruit prefrontal and occipital regions when accurately remembering objects. These findings support the cultural generalizability of longstanding theories of retrieval, such as cortical reinstatement (Johnson et al., 2009; Norman & O'Reilly, 2003) and retrieval monitoring in prefrontal cortex (Cruse & Wilding, 2009; Preston & Eichenbaum, 2013).

Although our data identified culture group differences in neural activity related to specific and general object memory, we cannot precisely determine which mechanisms account for these differences. We do not find strong evidence for cultural differences in mnemonic discrimination consistent with hippocampal pattern separation but it may be necessary to use high-resolution fMRI that

has the ability to distinguish subfields of the hippocampus in order to fully rule out that possibility. We speculate that some of our reported effects could reflect cultural differences in proneness to interference at retrieval or the tendency to use a novelty detection strategy, perhaps related to adoption of encoding vs. retrieval states. These candidate processes can be tested in future research. Furthermore, we cannot pinpoint the origin of these cultural differences. From a social orientation perspective, Americans' tendency to emphasise the self and individuality, particularly in autobiographical memories (Wang, 2001, 2006), may give rise to a remembering style that prioritises specific details. Cultural traditions of philosophy and logic, tracing back to ancient Chinese and Greek societies, differentially emphasise holistic, context-focused thinking versus analytic, object-focused thinking (Nisbett et al., 2001). Differences in physical environment may also play a role. One study found that images of Japanese cities, compared to American cities, contained more objects and that priming participants with Japanese city scenes induced greater attention to contextual, rather than focal, information (Miyamoto et al., 2006). Future work studying cultural differences in episodic memory could involve taking objective and subjective measures of participants' physical environment and testing the extent environmental factors (both real and perceived) relate to object memory, assessing variation across cultures. Assessing cultural differences across racial and ethnic groups would also be beneficial for future research, as would investigating groups exposed to multiple cultural influences (e.g., Chinese Americans; Chinese who have immigrated to the US, as in Gilliam & Gutchess, 2024). Cultural differences in object familiarity may also play a role in recognition. Although recent research extends findings of cultural differences in memory specificity to abstract stimuli (Leger et al., 2023), eliminating concerns about group differences in the familiarity or semantic meaningfulness of stimuli, it is possible that the real-world objects used in this study could be more familiar for one culture group than another. If so, this could influence neural activity at encoding and subsequent retrieval. The lack of object familiarity ratings from participants is a limitation of the present study, and the inclusion of these measures in future work would aid interpretation of cross-cultural memory effects.

Overall, the present study shows culture differences in neural activity for both specific and general object memory. Although univariate mnemonic discrimination analyses did not reveal significant clusters of cultural difference, correlations with behavioural discriminability and parametric modulation analyses indicate cultural differences in fusiform gyrus and parietal cortex, suggesting cultural effects in both perceptual and attentional processes that support retrieval. The approach taken in this study, which investigated both cultural differences and similarities, is important for achieving a complete and nuanced understanding of the extent different retrieval processes can be shaped by culture. Knowing whether previously-held assumptions about retrieval hold true for different populations is critical for the field of cognitive neuroscience, and future research on episodic memory should consider how the shared, cultural experiences shape the brain and behaviour.

#### Notes

- Resting state data constitute a separate publication: Zhang, W., Andrews-Hanna, J, Mair, R., Goh, J. O. S., & Gutchess, A. (2022). Functional connectivity with medial temporal regions differs across cultures. *Cognitive, Affective, & Behavioral Neuroscience, 22,* 1334–1348. https://doi.org/10.3758/s13415-022-01027-7
- These data constitute a separate publication: Lee, C. Y., Chen, C. C., Mair, R. W., Gutchess, A., & Goh, J. O. S. (2021). Culturerelated differences in the neural processing of probability during mixed lottery value-based decision-making. *Biological Psychology*, *166*, 108209. https://doi.org/10.1016/j.biopsycho. 2021.108209

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# Data availability statement

Data are available upon reasonable request.

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