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# Holistic versus feature-based binding in the medial temporal lobe

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#### ABSTRACT

A central question for cognitive neuroscience is how feature-combinations that give rise to episodic/source memories are encoded in the brain. Although there is much evidence that the hippocampus (HIP) is involved in feature binding, and some evidence that other brain regions are as well, there is relatively little evidence about the nature of the resulting representations in different brain regions. We used multivoxel pattern analysis (MVPA) to investigate how feature combinations might be represented, contrasting two possibilities, feature-based versus holistic. Participants viewed stimuli that were composed of three source features – a person (face or body), a scene (indoor or outdoor), and an object (bike or luggage) - which were combined to make eight unique stimulus identities. We reasoned that regions that can classify the eight identities (a multiclass classification) but not the individual features (a binary classification) likely have a holistic representation of each identity. In contrast, regions that can classify the eight identities and can classify each feature are likely to contain feature-based representations of these identities. To further probe the extent of feature-based or holistic classification in each region, we developed and validated a novel approach that directly compares binary and multiclass classification. We found clear evidence for holistic representation in the parahippocampal cortex (PHC), consistent with theories that posit that pattern-separation-like binding mechanisms are not unique to the HIP. Further clarifying the mechanisms of feature binding should benefit from systematic comparisons of multi-feature representations and whether they vary with task, type of stimulus, and/or experience.

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#### 1. Introduction

Episodic memory is characterized by remembering experiences as unique combinations of features, for example, what happened, where, and with whom (Johnson & Raye, 1981; Tulving, 1972; Underwood, 1969). A fundamental question for cognitive neuroscience is how such features are combined (i.e., bound) during encoding to later form the basis of the subjective experience of remembering, which entails context

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(Mandler, 1980) or source (Johnson, Hashtroudi, & Lindsay, 1993) memory. Theories of episodic/source memory and medial temporal lobe (MTL) function have long ascribed the hippocampus (HIP) a central role in mnemonic binding (Cohen, Poldrack, & Eichenbaum, 1997; Davachi, 2006; Johnson & Chalfonte, 1994; O'Reilly & Rudy, 2001; Ranganath, 2010; Squire, Stark, & Clark, 2004). For example, there have been several variations of the idea that the HIP establishes associations among features that are initially represented in other brain regions [e.g., objects in perirhinal cortex (PRC) and spatial location in parahippocampal cortex (PHC); Eichenbaum, Yonelinas, & Ranganath, 2007; Howard, Kumaran, Olafsdottir, & Spiers, 2011]. However, there is increasing evidence that regions other than HIP also support mnemonic binding. Thus, recent discussions have shifted from whether the HIP uniquely subserves feature binding to what differentiates the nature of bound representations in different MTL regions, for example, the types of information that are bound, and/or the way information is bound (Cowell, Bussey, & Saksida, 2010; Norman, 2010; Shimamura, 2010).

Advances in understanding potential functional divisions of the MTL require a clearer characterization of the nature of feature binding. In approaching this task, we assume that different regions of the brain likely represent different combinations of features. For example, the fusiform face area (FFA) is thought to represent combinations of face parts (Liu, Harris, & Kanwisher, 2010; McCarthy, Puce, & Belger, 1999), the PRC to represent combinations of object parts (Erez, Cusack, Kendall, & Barense, 2016), and the PHC to represent associations among elements of a scene (Aminoff & Tarr, 2015). Rather than ask whether a region represents a particular feature or feature combination, we ask how particular features are combined in various regions. One possibility is that the HIP is unique in the way in which it forms multifeature representations (Marr, 1971; O'Reilly & McClelland, 1994). Another possibility is that there are similar binding mechanisms throughout the MTL and it is the content of what is bound that varies across regions (Cowell et al., 2010; Shimamura, 2010).

Here we consider two possibilities of how feature combinations may be represented – in a *feature-based* manner or *holistically*.<sup>1</sup> In a feature-based representation, the featurecombination is completely predicted by the features (i.e., the whole is simply a combination of parts). If a region contains feature-based representations, it should be able to classify each feature (e.g., Persons A vs B, and Locations X vs Y) and the identity of the feature combination (e.g., AX vs AY vs BX vs BY). In a holistic representation, the feature-combination is represented in a way that is independent of each feature/part representation. If a region contains holistic representations, it should be able to classify the identity of a feature combination despite poor classification of the features themselves. We used simulations to validate this spectrum of feature-based versus holistic representation (Supplemental Material). Note that one's research question will largely determine how features and feature combinations are defined; here we used combinations of people, objects, and scenes as they are common source features of episodic memories.

There is reason to believe that HIP might form holistic representations of complex feature-combinations. For example, the Complementary Learning Systems (CLS) model (Marr, 1971; McClelland & Goddard, 1996; McClelland, McNaughton, & O'Reilly, 1995; Norman, 2010; Norman & O'Reilly, 2003) proposes that incoming features are bound within the HIP such that each feature combination is represented by an independent set of neurons, yielding separate representations for similar experiences (pattern separation). The CLS model has been used to predict that representations for similar experiences should be more distinct in HIP compared to other regions (Yassa & Stark, 2011). However, an important aspect of pattern separation is that independent neurons represent each multi-feature event so that experiences are orthogonally represented (i.e., holistically represented) rather than in a way that is systematically based on features. Therefore, while evidence that pairs of stimuli are represented distinctly in the HIP (e.g., Bakker, Kirwan, Miller, & Stark, 2008; Lacy, Yassa, Stark, Muftuler, & Stark, 2011; LaRocque et al., 2013; Motley & Kirwan, 2012) is consistent with pattern separation, it does not necessarily mean that the way in which the HIP forms such distinct multi-feature representations is through pattern separation. Another possibility is that the information represented in the HIP is more distinctive because it binds representations from lower in a processing hierarchy, such as item to item or item to spatial context (Cowell et al., 2010; Shimamura, 2010). By this logic, binding in the HIP and regions lower in the hierarchy could occur via similar mechanisms, which could yield holistic or feature-based representations.

Investigations of the types of content represented in the MTL suggest the presence of holistic representation in HIP. Across studies, it appears that the HIP contains reliable representations of individual stimuli/memories but not categorylevel information. Specifically, MTL cortex is much better than the HIP at discriminating stimulus categories (e.g., faces, objects, scenes) (Huffman & Stark, 2014; Liang, Wagner, & Preston, 2013; Martin, McLean, O'Neil, & Köhler, 2013). Nonetheless, the HIP is relatively good at discriminating different allocentric spatial locations (Hassabis, Chu, Rees, Weiskopf, Molyneux & Maguire, 2009), similar memories of movie clips (Chadwick, Hassabis, & Maguire, 2011; Chadwick, Hassabis, Weiskopf, & Maguire, 2010), and the perceived stimulus of two alternatives when a 50% morph is shown in a forcedchoice discrimination task (Bonnici et al., 2011). Together, these findings argue against the idea that the HIP detects differences between stimuli merely because it contains more information than other regions. However, additional studies examining representations of features and featurecombinations in a single experiment are required to more directly compare feature and identity information in these regions.

One functional magnetic resonance imaging (fMRI) study of MTL activity during remembering used such an approach (Chadwick et al., 2011). Participants viewed four video clips containing one of two events (a character walking while

<sup>&</sup>lt;sup>1</sup> Note that we use the term holistic not to refer to the completeness of an episodic memory (as in Horner, Bisby, Bush, Lin, & Burgess, 2015) but instead to refer to the fact that feature-combinations are not purely a function of individual features.

folding a jacket, or walking while carrying an umbrella) within one of two scenes (two different storefront backdrops). Participants studied these four video clips repeatedly until they could vividly recall each. They were then scanned while recalling each clip many times. The HIP, but not PRC, PHC, or entorhinal cortex (ERC), could classify which of the four clips was being remembered. Only the HIP could classify the scene (i.e., storefront) being recalled, and no MTL region could classify event content (i.e., jacket or umbrella event). To determine if the successful 4-way classification in HIP was merely due to scene information, Chadwick et al. examined the errors made in the 4-way classification. They found that the classifier was equally likely to misclassify the event, misclassify the scene, or misclassify both, suggesting that 4way classification was not simply due to relatively high scene classification. These results are consistent with holistic memory representations in the HIP.

Some studies have found evidence consistent with holistic representations outside the HIP. First, object-evoked activity in lateral occipital cortex (LOC) and PRC is more than just the sum of their activity to individual features (Erez et al., 2016). In that study, objects with different feature combinations were presented (A, B, C, AB, AC, BC). Researchers then calculated theoretical responses to full-featured objects (ABC) by adding the responses to the simpler objects (e.g., AB + C). They then compared different kinds of theoretical ABC responses (e.g., AB + C vs A + BC). They reasoned that if a region's response to an object is purely the sum of its response to the object's features, then there should be little difference between AB + C and A + BC. Using this approach, they found that both LOC and PRC responded differently to different arrangements of the same features, suggesting that object representations in these regions are not just coding the presence of a set of particular object features (A, B, C). While these results are interesting, it is important not to limit the definition of feature-based representations to those based on a simple sum of neural activity. For example, MacEvoy and Epstein (2011) used multivoxel pattern analysis (MVPA) to examine how scenes are represented in the parahippocampal place area (PPA) and LOC. Participants viewed scenes from four categories (kitchen, bathroom, intersection, and playground) and objects that are typical of each scene (refrigerator, oven, bathtub, toilet, car, traffic signal, slide, and swing set). Not surprisingly, patterns of activity in PPA elicited by the individual objects could be used to classify object category and those elicited by the whole scenes could be used to classify the scene category. Interestingly, a classifier trained on PPA activity elicited by individual objects could not classify scene category. These results suggest that the PPA contains representations of scenes that are more than just object-based. A second finding suggesting holistic representation outside the HIP comes from a recent study by Coutanche and Thompson-Schill (2015). Patterns of activity in anterior temporal lobe (ATL) could classify four imagined food-types (tangerine, carrot, lime, and celery) but not their characteristic features (color and shape). This suggests that the ATL contains holistic rather than feature-based object representations. Taken together, these studies provide preliminary evidence that holistic representations can be found outside the HIP and even outside MTL.

While the results of these studies comparing feature and identity classification are consistent with the idea that certain regions contain holistic representations, two caveats remain when applying these findings to the current question. First, in the case of Chadwick et al. (2011) and Coutanche and Thompson-Schill (2015), it remains possible that abovechance identity classification was based on feature classification that did not reach significance at the threshold used (e.g., classifying A1 vs A2 at 53%, and B1 vs B2 at 52% may yield small but significant 4-way classification of A1B1, A1B2, A2B1, and A2B2). The current experiment includes a novel analysis that addresses this possibility. Second, both MacEvoy and Epstein (2011) and Coutanche and Thompson-Schill (2015) found identity representations that were more than a combination of the examined features (i.e., objects in the PPA, and color and shape in the ATL), but some features were not examined. For example, PPA representations of scenes may be based on object and layout features (Harel, Kravitz, & Baker, 2013; Kornblith, Cheng, Ohayon, & Tsao, 2013; Kravitz, Peng, & Baker, 2011) and the representation of layout was not examined. While it is impossible to examine every possible feature, the current experiment used individual stimuli that are purely re-combinations of specific feature elements. If identity classification exists in the absence of feature classification under these conditions, we can be relatively confident that identities are represented holistically.

In summary, different regions of the MTL likely represent feature-combinations of varying types, but it is unclear how these combinations are represented. To address this question, we showed participants eight pictures that were constructed with three source features: a scene feature (outdoor or indoor), an object feature (bike or luggage), and a person feature (face or body). We assessed whether different regions in MTL contain holistic or feature-based representations of these complex combinations of visual features. In addition to providing information that should help clarify the nature of representations resulting from feature binding, the outcome should provide evidence relevant to models emphasizing the uniqueness of hippocampal representation, such as the CLS model (O'Reilly & McClelland, 1994), and models that posit that binding mechanisms similar to those operating in HIP operate outside the HIP (Cowell et al., 2010; Shimamura, 2010).

#### 2. Material and methods

#### 2.1. Participants

Participants were members of the Yale/New Haven community who gave written, informed consent in accordance with the Yale Human Investigations Committee. All participants had normal or corrected-to-normal vision and no history of neurological or psychiatric illness. Data from 25 participants (17 females, mean age =  $23.4 \pm 3.9$  years) were analyzed. Data from 5 additional participants were excluded for movement (2), technical difficulties during scanning (2), or finishing too few runs to analyze (1). Excessive movement was defined as having more than 50 TRs for which the Euclidean norm of the motion derivative exceeded 1.0.

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#### 2.2. Experimental procedure

During fMRI, participants viewed each of eight pictures a number of times (duration = 2 sec, ISI = 6, 8, or 10 sec; Fig. 1B). As shown in Fig. 1A, the pictures were constructed from three features: a scene feature (outdoor or indoor), an object feature (bike or luggage), and a person feature (face or body). To encourage participants to attend to all of the features on every trial, and to engage event processing, they were asked to indicate how many times they had seen that particular picture so far in the current scanning run (1-4). Participants were allowed to make their response at any point the picture was on the screen. Each picture was shown 4 times in each of 10 runs, for a maximum of 40 instances of each stimulus (eighteen participants completed 10 runs, six completed 9 runs, and one participant completed 8 runs). The maximum number of runs were conducted for a scan time slot given participants' arrival time, ease of setting them up, etc. For each participant, the order of the stimuli was generated using the optseq2 program (https://surfer.nmr.mgh.harvard.edu/ optseq).

#### 2.3. fMRI acquisition & preprocessing

Data were acquired using a Siemens Trio TIM 3.0T scanner and a 32-channel head coil. Functional images were collected

using multi-band echo planar imaging [parameters: repetition time (TR) = 2,000 msec, echo time (TE) = 32 msec, flip angle  $\alpha = 62^{\circ}$ , field of view (FOV) = 200 mm, matrix = 100 × 104, slice thickness = 2 mm, 69 slices aligned with the long axis of the HIP, multi-band factor = 3]. High-resolution images were acquired using a 3D MP-RAGE sequence (TR = 2530 msec, TE = 2.77 msec,  $\alpha = 7^{\circ}$ , FOV = 256 mm, matrix = 256 × 256, slice thickness = 1 mm, 176 slices).

fMRI data were preprocessed using the Analysis of Functional Neuroimages (AFNI; Cox, 1996) software package (http://afni.nimh.nih.gov/afni). The first 4 volumes (8 sec) of each functional dataset were discarded to allow the signal to reach steady-state magnetization. Motion correction and alignment were completed with a single transformation: functional volumes were aligned to each other and to each individual's high-resolution anatomical scan in one transformation. Each voxel's time series was scaled (within runs) to a mean of 100 and a maximum of 200 to allow betas to more closely reflect percent signal change. The data were not spatially smoothed.

#### 2.4. Regions of interest

Regions of interest were defined using FreeSurfer's automatic volumetric segmentation (http://surfer.nmr.mgh.harvard. edu/) with a probability threshold of 50% (Fig. 2). We defined



Fig. 1 – The eight stimuli corresponding to the eight combinations of three source features: face or body, bike or luggage, and indoor or outdoor. Pictures were shown one at a time for 2 sec, with a 6-10 sec jittered inter-trial-interval. During the last second of the ITI, the fixation cross disappeared to cue the upcoming stimulus.



Medial Temporal Lobe

Face-Selective Regions

Scene-Selective Regions

Fig. 2 — Eight of eleven regions of interest (not shown: fusiform cortex, lateral occipital cortex, and intraparietal sulcus) for a representative participant. Regions of interest were generated using FreeSurfer's automated cortical segmentation (see text).

6 anatomical ROIs in occipitotemporal cortex and MTL: LOC, fusiform cortex (FUS), PHC, defined as the posterior half of the FreeSurfer parahippocampal cortex label, PRC, defined as the anterior half of the FreeSurfer parahippocampal cortex label, ERC, and HIP. The LOC was included because of its object sensitivity (Malach et al., 1995) and the fusiform was included because it includes face-selective cortex (Kanwisher, McDermott, & Chun, 1997; McCarthy, Puce, Gore, & Allison, 1997). Custom Matlab scripts filled very small gaps in the automatic FreeSurfer ROIs, and visual inspection with minor manual edits ensured precise anatomical coverage. Voxels at the border of two ROIs and assigned to both (e.g., PHC and HIP) were excluded from the analysis. All anatomical ROIs were bilateral.

We also defined 5 additional functional ROIs, as positive controls, using a probability atlas of face and scene responses. The probability atlas was developed in a previous study (Engell & McCarthy, 2013) that examined BOLD responses to faces, scenes, houses, and both biological and non-biological motion in localizer data from over 100 participants. The atlas contains, at each voxel, the percentage of participants who showed a category-sensitive response (defined by a zscore of ±1.65 in the localizer contrast) to either faces or scenes. The peak voxels within unique clusters of a given contrast (i.e., face > scene or scene > face) were identified, corresponding to peaks within regions known as the right occipital face area (rOFA), the right fusiform face area (rFFA), the PPA, bilateral, the intraparietal sulcus (IPS, bilateral) and retrosplenial cortex (RSC, bilateral). Finally, a small sphere was then centered around this peak voxel to define each of the 5 functional ROIs (radius 3 mm for face-peaks, 7 mm for scene-peaks). We focused on the right, as opposed to left FFA because of the known right hemisphere bias for face processing (Kanwisher et al., 1997; McCarthy et al., 1997; Rossion, Hanseeuw, & Dricot, 2012).

#### 2.5. Classification analyses

We estimated activity for each trial within each voxel using AFNI's 3dREML. Motion parameters and 1st, 2nd, and 3rd order polynomials (drift) were included as nuisance regressors. Beta estimates were normalized within each stimulus category for a given classifier (e.g., within Faces and Bodies for a Face vs Body discrimination). All classification analyses used a Gaussian Naïve Bayes (GNB) classifier implemented in PyMVPA (Hanke et al., 2009). GNB classifiers are relatively good at classification problems with small training samples (Mitchell, Hutchinson, Niculescu, Pereira, & Wang, 2004; Singh, Miyapuram, & Bapi, 2007). A leave-one-run-out crossvalidation scheme was used.

We conducted 7 different classification analyses: three 2way classifications for each of the individual features (e.g., face vs body), three 4-way classifications for each feature pair (e.g., indoor-face vs indoor-body vs outdoor-face vs outdoorbody), and one 8-way classification for the feature triplet (indoor-face-bike vs indoor-face-luggage vs indoor-body-bike vs indoor-body-luggage vs outdoor-face-bike vs outdoor-faceluggage vs outdoor-body-bike vs outdoor-faceluggage vs outdoor-body-bike vs outdoor-body-luggage). Multiclass classification was implemented using a one-against-all scheme (e.g., Tatsumi, Tai, & Tanino, 2011) to avoid multi-way classification being based on any one of the three features.

For each classification analysis, we compared accuracy to chance (~50% for 2-way, ~25% for 4-way, and ~12.5% for 8-way) using permutation testing. For each participant, class labels were shuffled 100 times and classification was done on each of the shuffled sets of labels. (The mean of these 100 permutations determined the chance level used to baseline Actual 8-way classifier performance in Fig. 4). We then calculated a null group mean accuracy by randomly selecting a value for each participant from their set of shuffle-based accuracies and taking the average. We created a group null distribution by calculating this group null mean 10,000 times. The real group mean was compared to this null distribution to obtain a two-tailed *p*-value.

We first asked whether there was significant 8-way classification in the absence of significant 2-way classification, which would suggest holistic rather than feature-based representation of stimulus identity. Although unlikely, it is possible that 2-way classification that did not reach significance might accumulate to yield minimal, but significant, 8way classification. Therefore, we developed a novel way to directly compare binary and multiclass classification. To begin, we computed a Synthetic 8-way classifier that was based on the 2-way classifiers. For each participant, we took their 2-way classifier accuracies (e.g., Face vs Body = 60%, Indoor vs Outdoor = 55% and Bike vs Luggage = 50%) and



Fig. 3 – Average response for each presentation condition. Error bars are  $\pm 1$  standard error of the mean.

multiplied them to generate a 2-way-based Synthetic 8-way accuracy (e.g., 60%\*55%\*50% = 16.5%). As with the actual classifiers, chance was determined empirically using permutation testing. Because the purpose of the Synthetic classifier was to control for identity classification that was due to feature information, permutations involved shuffling labels so that identity information was preserved but feature information was destroyed. Specifically, labels were shuffled across, but not within, identities (e.g., all Face-Indoor-Bike trials might be re-labeled as Body-Indoor-Luggage trials). Any lingering identity information found by the Synthetic classifier after shuffling would be based on something other than feature information. The higher performance of the Synthetic classifier in unshuffled data compared to the shuffled data then reflects the amount of feature information in a region. Permutations were done 100 times for each subject. The mean of these 100 permutations determined the chance level used to baseline Synthetic classifier performance in Fig. 4.

Finally, we directly compared Actual and Synthetic 8-way classifier performance using a paired sample t-test. Because the Actual and Synthetic 8-way classifiers may have slightly different levels of chance, we again used permutation tests to create a null t-distribution and obtain a *p*-value for the paired sample t-test. For each participant, we randomly selected one of their 100 permutation-derived Synthetic classifier accuracies and one of their 100 permutation-derived Actual classifier accuracies. A paired sample t-test then compared these Actual and Synthetic scores across the 25 participants. We repeated this 10,000 times to build a null t-distribution. The t-value from the unshuffled data analysis was compared to this null t-distribution to obtain a two-tailed *p*-value.

#### 3. Results

#### 3.1. Behavioral results

Participants' average frequency judgments for each presentation number are shown in Fig. 3. For example, if a participant responded "1" to half of the 2nd presentation trials, and "2" to the other half, their average frequency judgment for 2nd presentation trials would be 1.5. As evident in Fig. 3, participants' average frequency judgments increased as the true presentation number increased [F(3,21) = 52.76, p < .001]. The mean proportion of items at each presentation frequency for which judgments were accurate were: 1st presentations = .70 (SD = .13), 2nd presentations = .50 (SD = .16), 3rd presentations = .46 (SD = .12), and 4th presentations = .66 (SD = .20).

#### 3.2. Classification results

Table 1 shows the results of the 2-way and 8-way classification analyses for regions outside the MTL. Each feature could be classified in the ROIs known to process that category and in some additional visual regions. Face versus Body (person) features were classified above chance in FUS, rOFA, rFFA, as well as in LOC, IPS. Indoor versus Outdoor (scene) features were classified above chance in PPA, RSC, IPS, as well as in FUS, LOC, and rOFA. Bike versus Luggage (object) stimuli were classified above chance in LOC, as well as in FUS, rOFA, and



Fig. 4 – Actual versus Synthetic 8-way performance (% above empirically derived chance). Error bars are ±1 standard error of the mean, provided for information (but see description of permutation tests in text used to determine significance). Significant differences at an alpha of .05 are marked with an \* while marginal differences at an alpha of .10 are marked with a ~. FUS = fusiform cortex; LOC = lateral occipital cortex; rOFA = right occipital face area; rFFA = right fusiform face area, PPA = parahippocampal place area; RSC = retrosplenial cortex; IPS = intraparietal sulcus; HIP = hippocampus; ERC = entorhinal cortex; PRC = perirhinal cortex; PHC = parahippocampal cortex.

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Region	Face versus Body	Indoor versus Outdoor	Bike versus Luggage	Actual 8-way
FUS	M = 73.31; <i>p</i> < .001	M = 53.54; <i>p</i> < .001	M = 53.64; <i>p</i> < .001	M = 21.46; <i>p</i> < .001
LOC	M = 78.95; p < .001	M = 54.21; <i>p</i> < .001	M = 60.52; <i>p</i> < .001	M = 28.34; p < .001
rOFA	M = 62.77; p < .001	M = 52.00; p = .002	M = 53.38; p < .001	M = 16.11; <i>p</i> < .001
rFFA	M = 56.98; p < .001	M = 50.30; p = .841	M = 50.93; p = .174	M = 14.85; <i>p</i> < .001
PPA	M = 50.78; p = .246	M = 51.64; p = .007	M = 50.80; p = .242	M = 13.97; <i>p</i> < .001
RSC	M = 49.86; p = .839	M = 51.89; p = .002	M = 49.18; p = .213	M = 13.23; p = .090
IPS	M = 53.81; <i>p</i> < .001	M = 53.08; <i>p</i> < .001	M = 52.16; <i>p</i> < .001	M = 13.96; <i>p</i> < .001

Table 1 – 2-Way and 8-way classification accuracy versus chance in visual cortex.

IPS. Table S1 shows the results of the 4-way classification analyses.

Table 2 shows the results of the 2-way and 8-way classification analyses for regions in the MTL. The PHC showed significant 8-way classification despite non-significant 2-way classification (classification of objects was below chance), indicating the presence of holistic representations. This signature of holistic representation did not occur for any other region. However, simply seeking the presence and absence of significance across multiple analyses may have limited our ability to detect holistic representations. For example, the HIP had marginally significant (p < .076) 8-way classification despite overall fairly poor performance on the 2-way classifiers. We therefore compared Actual and Synthetic (featurebased) 8-way classifier performance in each region (Fig. 4, Table S2). Again, we found evidence of holistic representation in PHC as Actual 8-way classifier performance was significantly greater than Synthetic performance (Note that synthetic performance in PHC was particularly low in part because of anti-classification of objects in the region. Some may see this as causing an artificial difference between the actual and synthetic classifier performance. However, we think the anti-classification of objects in PHC would make it all the more difficult to achieve purely feature-based significant 8-way classification). This more direct test of holistic representation did not provide evidence for holistic representation in HIP (see Discussion). Interestingly, Actual 8-way was significantly less than Synthetic 8-way performance in rOFA, suggesting that features are more discriminable in this region when considered in isolation rather than in combination.

Of course, it is possible that features other than those manipulated contributed to classifier performance. For example, 8-way identity classification might arise from the difference between the contour of a face against the dock and the contour of a face against the living room carpet. If *lowerlevel* features support 8-way identity classification, we would expect low-level information to contribute to significant Person, Scene, and Object classification. This might be the case in the LOC, where there was significant feature information and marginally significant Actual versus Synthetic classification. Importantly, the PHC did not have significant 2-way classification, suggesting that the 8-way identity classification in that region was not due to low-level features that differentiate each picture.

In summary, the PHC contained identity information in the absence of feature information, and the amount of identity information was above and beyond what would be expected based on the amount of feature information in the region.

#### 4. Discussion

This study addressed a relatively unexplored but fundamental question about how events are represented in the MTL. We asked whether the source feature combinations that make up complex events are represented in a holistic or feature-based manner. Using MVPA of activity associated with systematic combinations of person, place, and object features, we found a number of regions (FUS, LOC, rOFA, rFFA, PPA, IPS, and PHC) that were able to classify among 8 stimulus identities, but only the PHC was able to do so in the absence of significant feature information (person, place, object). Furthermore, identity classification in the PHC was significantly greater than what would be expected based on the amount of feature information in the region (i.e., Synthetic identity classification), providing evidence that the PHC represented these stimuli holistically. Our results extend investigations of MTL function by moving beyond defining 'what' is represented 'where' in the brain to beginning to answer questions about the nature of these representations.

Specifically, our finding of holistic representations of scene-object-person information in PHC indicates that pattern-separation-like binding mechanisms occur outside HIP (Cowell et al., 2010; Shimamura, 2010), and provide further information about the types of information that PHC can holistically bind. These findings augment previous findings that the ATL and PPA contain identity representations that are not purely a function of object or scene features, respectively (Coutanche & Thompson-Schill, 2015; MacEvoy & Epstein,

Table 2 – 2-Way and 8-way classification accuracy versus chance in medial temporal lobe.

Region	Face versus Body	Indoor versus Outdoor	Bike versus Luggage	Actual 8-way
HIP	M = 51.17; p = .054	M = 50.48; p = .476	M = 49.27; p = .258	M = 13.28; p = .076
ERC	M = 50.64; p = .221	M = 50.72; p = .270	M = 48.84; p = .072	M = 12.55; p = .981
PRC	M = 50.43; p = .525	M = 50.95; p = .134	M = 49.36; p = .284	M = 11.86; p = .104
PHC	M = 49.15; p = .242	M = 50.58; p = .334	M = 48.36; p = .006	M = 13.58; p = .014

2011). Our design extends this work by controlling combinations of three specific features that varied across stimulus identities, and suggests the value, in future studies, of directly comparing in different brain regions feature and identity representations that occur under common task conditions.

The relatively poor feature classification in HIP adds to previous findings that HIP does not contain strong category information (Huffman & Stark, 2014; Liang et al., 2013; Martin et al., 2013). However, our findings in the HIP are inconclusive with regard to holistic versus feature-based representation -HIP identity classification was close to significant despite only containing significant classification of one of the three features (i.e., the person feature). Similarly, Chadwick et al. (2011) found that the HIP could classify memories composed of events and background scenes despite containing scene but not event feature information. Evidence for holistic representation in that study was more compelling than in the current study because identity classification did not seem to simply be a byproduct of scene classification. When we specifically tested whether identity classification was a byproduct of feature information in our study, identity classification in HIP was not higher than would be expected based on feature information in the region (i.e., Synthetic identity classification, Table S2). There are several possible reasons that we found less conclusive evidence for holistic representation in HIP than Chadwick et al. (2010). We directly compared binary and multiclass classification using a Synthetic 8-way classifier, and this was a more stringent test of holistic representation. Also, our experiment examined feature and identity representation for a different set of features. Although it is generally assumed that HIP binds features in a domain general way, sensitivity to detecting characteristics of hippocampal function likely varies with feature set, task context, and other factors. Notably, we examined feature-combination representation while each of eight distinct pictures were perceptually present (i.e., a recognition task) whereas Chadwick et al.'s participants were remembering four well-learned short videos when cued with a still from the video (a recall task). Finally, our multiple feature but single picture stimuli may have evoked holistic scene representation in PHC while the temporally-extended events used as stimuli in Chadwick et al., may have made it easier to detect holistic representation in HIP (e.g., see Hsieh, Gruber, Jenkens & Ranganath, 2014, for evidence of hippocampal representation of joint item and temporal information).

Even if we had found significant evidence for holistic representation in HIP, evidence for holistic representation in PHC is inconsistent with the idea that feature combinations are uniquely represented by pattern separation in HIP (Marr, 1971; McClelland & Goddard, 1996; McClelland et al., 1995; Norman, 2010; Norman & O'Reilly, 2003). While other fMRI studies have found distinct representations within the HIP (Bakker et al., 2008; Lacy et al., 2011; LaRocque et al., 2013; Motley & Kirwan, 2012), only a few have examined whether the nature of multi-feature representations in the HIP is unique, namely more sparse than in other regions (e.g., Hulme, Skov, Chadwick, Sibner, & Ramsoy, 2014; Wixted et al., 2014). Given that the CLS model specifically localizes pattern separation to the dentate gyrus, it would be interesting in future studies to use a scan protocol that identifies separate HIP subregions to

see if evidence for holistic representation in HIP is specific to dentate gyrus, and/or how the type of representation in HIP and other brain areas is affected by paradigms that promote or inhibit pattern separation (e.g., Duncan, Sadanand, & Davachi, 2012). Some such work suggests that holistic representations may be selectively present in the CA3 subfield of HIP when using a retrieval task (Chadwick, Bonnici, & Maguire, 2014).

A number of challenging open questions remain regarding how feature combinations are represented in different brain areas. Task demands may change the way in which feature combinations are represented. For example, color and object combinations can be processed separately as two components of a stimulus, or as a unitized combination of features (e.g., Staresina & Davachi, 2008; 2010). In other cases, a task may affect the salience of a feature or even generate an otherwise absent feature. For example, a set of artificial face identities may be defined by their gender, age, and expression. An orienting task that requires evaluating the trustworthiness of each face (Todorov, Mende-Siedlecki, & Dotsch, 2013) may cause face representations to include the trustworthiness judgment. In this case, faces might be represented in a way that is more than just gender + age + expression (i.e., holistically). On the other hand, the trustworthiness judgment could be defined as a feature itself (i.e., a cognitive operations feature, Johnson & Raye, 1981; Johnson, et al., 1993), rather than impetus for holistic representation. Clearly, the definition of what qualifies as holistic will vary based on how features are defined and the research question. Also important, expertise or experience may make certain feature combinations begin to be processed as a single whole rather than collection of parts. For example, statistical regularities can change how stimuli are represented in the MTL (Schapiro, Kustner, & Turk-Browne, 2012; Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013).

In other cases, the form of multiple-feature representations may be more influenced by the stimuli and which brain regions are considered than the psychological context (e.g., task or previous experience) of the participant. For example, it is likely that how features are defined will partially determine whether a region contains holistic representations. Object sensitive regions may contain holistic representations of object parts, face sensitive regions of face parts, language sensitive regions may contain holistic representations of visual and auditory language information, etc. In some cases, holistic representation may even be an intrinsic property of the feature combinations themselves, for example in the case of gestalt illusions (Kubilius, Baeck, Wagemans, & Op de Beeck, 2015). Finally, holistic representation may be an intrinsic property of the anatomical or computation characteristics of a given brain region – as is predicted for the dentate gyrus by computational models (Marr, 1971; McClelland & Goddard, 1996; McClelland et al., 1995; Norman, 2010; Norman & O'Reilly, 2003).

Understanding how features are bound together is central to understanding the mechanisms by which source features are encoded and activated, giving rise to the subjective experience of episodic memory. Approaches similar to the one we used here should be useful to further characterize the conditions under which holistic or featurebased representations are observed. Is there something

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special about the computational and anatomical properties of MTL regions that allow them to represent unique stimuli? Are the 'unitized' representations posited in PRC (Diana, Yonelinas, & Ranganath, 2007) similar in type to those in PHC or other brain regions? Answers to these questions depend on continuing to refine our characterization of what is meant by source features, feature binding, and multifeature representations.

In conclusion, we examined a specific hypothesis about how feature combinations are represented in the brain. We found evidence for holistic representations, as opposed to feature-based representations, in PHC, contributing to further understanding of the nature of scene representation in this region. As cognitive neuroscience continues to examine content representation using MVPA, it will be informative to systematically compare the type of multi-feature representations in different brain regions, and determine whether this varies with task, stimulus type and/or experience.

#### Author contributions

R.N.V. designed the experiment, collected data, developed and conducted the analyses, and wrote the manuscript. G.M. and M.K.J. advised on experimental design, analyses and writing.

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#### Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.cortex.2017.01.011.

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