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Temporal lobe contribution to perceptual function: A tale of three patient groups

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ABSTRACT

There has been growing recognition of the contribution of medial and anterior temporal lobe structures to non-mnemonic functions, such as perception. To evaluate the nature of this contribution, we contrast the perceptual performance of three patient groups, all of whom have a perturbation of these temporal lobe structures. Specifically, we compare the profile of patients with focal hippocampal (HC) lesions, those with more extensive lesions to the medial temporal lobe (MTL) that include HC and perirhinal cortex (PrC), and those with congenital prosopagnosia (CP), whose deficit has been attributed to the disconnection of the anterior temporal lobe from more posterior structures. All participants completed a range of'oddity' tasks in which, on each trial, they determined which of four visual stimuli in a display was the'odd-one-out'. There were five stimulus categories including faces, scenes, objects (high and low ambiguity) and squares of different sizes. Comparisons were conducted separately for the HC, MTL and CP groups against their matched control groups and then the group data were compared to each other directly. The group profiles were easily differentiable. Whereas the HC group stood out for its difficulty in discriminating scenes and the CP group stood out for its disproportionate difficulty in discriminating faces with milder effects for scenes and high ambiguity objects, the MTL group evinced a more general discrimination deficit for faces, scenes and high ambiguity objects. The group differences highlight distinct profiles for each of the three groups and distinguish the signature perceptual impairments following more extended temporal lobe alterations.

In the recent reconsideration of the role of the hippocampus and neocortex, Moscovitch and colleagues (Moscovitch et al., 2016) note that the medial temporal lobe structures play a role in non-mnemonic functions, such as perception, problem solving, decision-making and language. Here, we address this exact issue, specifically with respect to perception, and we dedicate this paper to Morris Moscovitch in recognition of his profound contribution to science, to his students and to his colleagues.

1. Introduction

Theories regarding the role of the medial portions of the temporal lobe have undergone substantial revision in the last few years. Whereas it has been well established that the medial temporal lobe (MTL), which comprises the hippocampus, and the entorhinal, perirhinal and parahippocampal cortices, plays a critical role in memory functioning, there is growing consideration of additional roles for these structures, particularly in relation to visual perception. Specifically, it has been claimed that the role of the MTL extends beyond the domain of long-term declarative memory to encompass a role in perception, with the hippocampus (HC) and perirhinal cortex (PrC) contributing to spatial and object perception, respectively [for review, see (Bussey and Saksida, 2005; Graham et al., 2010; Lee et al., 2012; Moscovitch et al., 2016)].

That these MTL structures are involved in complex perception is perhaps not surprising (Murray and Wise, 2010). First, many theories argue that because the PrC is at the apex of the ventral visual processing stream, it can form highly specific

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representations that disambiguate similar objects in both perceptual and mnemonic tasks (Murray and Bussey, 1999). Second, some of these regions, including the PrC, receive a convergence of information from modality-specific (unimodal) cortical fields across several sensory domains, as well as inputs from polymodal regions (Carmichael and Price, 1995; Friedman, Murray, O'Neill, and Mishkin, 1986; Suzuki and Amaral, 1994). Last, in addition to receiving visual inputs from area TE, the PrC has strong reciprocal connections with the hippocampal formation, amygdala, and prefrontal cortex (Furtak, Wei, Agster, and Burwell, 2007), and data from recent investigations have indicated that the hippocampus (HC) also contributes to processes beyond memory. In particular, with respect to visual perception, it has been demonstrated that the HC and the PrC are necessary for accurate perceptual discrimination of conjunctive scene and object/face stimuli, respectively, as revealed by neuropsychological investigations (Barense et al., 2005b; Graham et al., 2006; Lee et al., 2005a, 2005, 2005b). Humans with lesions affecting HC or MTL (the latter defined as damage encompassing both the HC and PrC) also are impaired at perceptual tasks: in one study, visual discrimination was evaluated in individuals with lesions to HC or with more extensive lesions to MTL (Lee et al., 2005b). Whereas the HC patients were significantly poorer at discriminating scenes than other stimulus classes (e.g. faces, objects, color), patients with MTL lesions were significantly impaired at discriminating most classes, with the exception of color.

Empirical findings to support an MTL contribution to perception also come from studies conducted with non-human primates, as well as from structural and functional neuroimaging studies with humans. For example, lesions to PrC in monkeys give rise to a deficit in face and object discrimination when the animals matched stimuli from different versus the same viewpoint (Buckley, Booth, Rolls, and Gaffan, 2001; Bussey, Saksida, and Murray, 2003). Functional MRI studies show activation of MTL during perception using tasks similar to those employed in the neuropsychological studies alluded to above, with differential recruitment of the HC and PrC for scene and object/face discriminations, respectively (Barense et al., 2010; Erez et al., 2015; Hodgetts et al., 2015; Lee et al., 2008; Mundy et al., 2013, 2012; O'Neil et al., 2009). Emerging investigations using diffusion MRI also reveal similar functional dissociations; using the same tasks as above, inter-individual differences in scene and face perceptual discrimination accuracy was associated with inter-individual variability in two white matter tracts connected to the HC and PrC, respectively (Hodgetts et al., 2015; Postans et al., 2014).

The finding that the MTL is engaged in perceptual tasks has been accounted for within a computational framework termed the'representational hierarchical model' (Saksida and Bussey, 2010) (Cowell, 2012). Specifically, the claim is that more caudal inferotemporal cortical regions (e.g., V4, TE/TEO) process simple features or basic object stimuli, while more rostral regions, including the PrC, process more complex conjunctions of stimulus features that mediate both object perception and memory. This computational account argues further that conjunctive representations, such as those required for discriminating between exemplars with many overlapping features, are implemented in these anterior/medial temporal structures (Graham et al., 2010; Murray et al., 2007; Saksida and Bussey, 2010). By contrast, discriminating between visual exemplars with minimal featural overlap can be supported by retrieval of lower-level features dependent upon posterior visual cortical regions (Mundy et al., 2012). Empirical data consistent with this model also comes from studies of human and non-human primates demonstrating that damage to PrC results in an impairment in discriminating objects, especially when features composing the objects are ambiguous (the same feature appeared in multiple objects) rather than non-ambiguous (each feature is unique to each object) (Barense et al., 2012a; Bussey et al., 2003; Lee et al., 2005b).

Thus, the claim is that the PrC is responsible for storing and processing representations of complex, feature conjunctive object stimuli and binding together these complex features within individual objects (see also (Barense et al., 2005b; Bussey and Saksida, 2002; Bussey et al., 2002; Erez et al., 2015)). The HC, too, is thought to play a role in binding conjunctions of features but, rather than binding features within an object, the proposed role of the HC is to bind relational information about objects and their context or spatial location or relations among the constituent elements of experience (Lee et al., 2005; Mitchell et al., 2000; Ranganath et al., 2004; Slotnick, 2010), even over extremely short delays (Burgess et al., 2002; Hannula et al., 2006; Olsen et al., 2012).

1.1. Congenital prosopagnosia

In the last several years, an account, which is not that dissimilar from the binding account offered above for MTL structures, has been offered to explain the perceptual difficulties in individuals with congenital prosopagnosia. Congenital prosopagnosia (CP) refers to the impairment in face recognition that is evident despite the individual having intact sensory and intellectual functions (Avidan et al., 2011; Behrmann and Avidan, 2005; Behrmann et al., 2005b; Bentin et al., 1999; Dobel et al., 2007; Duchaine et al., 2007; Le Grand et al., 2006) and in the absence of any neurological abnormality as evident on conventional MRI (no lesion, no other neurological explanation). Previous studies have revealed normal BOLD activation in CP in the posterior regions usually associated with face recognition, including the fusiform face area (FFA), occipital face area (OFA) and superior temporal sulcus (STS) (Avidan and Behrmann, 2009; Avidan et al., 2005; DeGutis, Bentin, Robertson, and D'Esposito, 2007; Hasson et al., 2003) (but see (Bentin et al., 2007; Furl et al., 2011; Hadjikhani and de Gelder, 2002; Minnebusch et al., 2009)), suggesting that prosopagnosia results from compromised connectivity between these more posterior structures and more anterior structures which are also engaged in face individuation, including in the anterior temporal lobe (for example, (Kriegeskorte et al., 2007; Rajimehr et al., 2009; Simmons et al., 2010)). The deficit in CP, then, is thought to arise from a disconnection of the anterior temporal lobe from other caudal regions. Evidence favoring this account is gleaned from structural imaging studies of CP showing reduced integrity of white matter fiber tracts projecting through the core face-selective regions to the anterior temporal lobe, but intact tracts in other regions (Thomas et al., 2009), as well as reduced volume in the anterior temporal cortex (Behrmann et al., 2007; Bentin et al., 1999) (but see (Song et al., 2015)). Also, consistent with the idea of a disconnection, recent fMRI data have shown that, relative to controls, activation in the anterior temporal lobe (ATL) is reduced in CP as is functional connectivity between the ATL and posterior regions such as FFA, OFA and STS (but not with the amygdala so not all anterior structures are affected (Avidan et al., 2014)). In CP, the dissociation between the ATL and posterior regions was evident under task-related conditions as well as under resting-state conditions i.e., in the absence of visual stimulation (for converging results in healthy individuals, see also (O'Neil et al., 2014)). Interestingly, a breakdown in the connectivity between more posterior fusiform and more anterior temporal and frontal lobe structures has also been implicated as the pathogenesis of primary progressive prosopagnosia (Grossi et al., 2014), offering additional evidence for this disconnection account.

Of particular relevance to the current paper, the coordinates for

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Table 1
Talairach coordinates from studies showing perception-related activation in ATL or PrC.

Region: right	Study	X	Y	Z
Anterior temporal lobe				
	(Avidan et al., 2014)	30	0	−33
	(Kriegeskorte et al., 2007)	38	2	−38
	(Pyles et al., 2013)	37	−7	−27
	(Von Der Heide et al., 2013)	29	−5	−31
	Mean	**33.5**	**−2.5**	**−32.25**
Perirhinal cortex				
	(Barense et al., 2010)	39	2	−36
	(Barense, Henson, and Graham, 2011)	38	−9	30
	(O'Neil et al., 2009)	33	−4	−26
	(Hodgetts et al. 2015)	28	−16	−32
	(Lee et al. 2008)	29	−9	−18
	(Mundy et al., 2013)	28	−7	−19
	(Lee et al., 2006b)	36	−16	−24
	Mean	**33**	**−8.4**	**−17.8**

the face-selective ATL identified in both the imaging studies of CP and of normal observers are very close to those demarcated as being the site of PrC, reflecting the anatomical complexity of the ATL and the difficulty in segregating regions and determining borders (Bonner and Price, 2013). Table 1 below shows the Talairach coordinates (mean of the x, y and z coordinates) gleaned from a selective overview of some existing studies of the region labeled as ATL and some of the studies of the region labeled as PrC. As evident from this table, although the two regions may diverge somewhat in the z-coordinates, the x-coordinates appear to overlap and the y-coordinates are rather close, as well, suggesting that these structures may be referenced interchangeably, at least in some studies. This anatomical proximity raises a question about whether the sites of altered function in the MTL patients described above (primarily from PrC damage) and that of the ATL in CP (primarily from disconnection) might be referring to a similar neural mechanism and locus. Further convergence between CP and MTL amnesia is provided by an investigation that reported impaired long-term memory for faces in individuals with one subtype of CP (Stollhoff et al., 2011a), revealing a potential mnemonic component in CP, as well (although, unsurprisingly, poor encoding of a face might result in long term memory deficits).

In addition to the possible anatomical overlap, there is also overlap in the explanation offered to account for the neuropsychological patterns in the different patient groups: the same computational alteration offered for the MTL cases, a deficit in combining features into more complex and unique patterns (see representational hierarchical account described above), has been offered for the deficit in face recognition in CP. Furthermore, given their extensive feature overlap, faces are the paradigmatic stimulus class (like the ambiguous objects used previously) that would engage these high-level visual MTL structures according to representational hierarchical accounts. In an assessment of the effect of the impact of reduced network connectivity (as in CP) on face perception, Stollhoff et al., (2011b) trained a neural network model to represent face images with two different algorithms: When a predisposition towards decreased network connectivity was implemented in the model, it resulted in a featural representation of faces with no opportunity for deriving conjunctions or higher-order statistics of the input, akin to the proposed mechanism underlying CP. In contrast, when the network was trained for optimal information encoding, it led to holistic representation and integration of the features across the whole face. The notion that CP results from the failure to derive higher-order conjunctions has been widely proposed and there are considerable empirical data to support this claim (Barton, 2008; de Gelder and Rouw, 2000). The account pivots on the notion that, because all faces differ only slightly in the shape and size of facial features, which are arranged in the same top-heavy configurations, the spatial relations among these features are particularly important for facial identity individuation (for a review, see (Maurer et al., 2002; Richler and Gauthier, 2014)), and it is these spatial relations (second order statistics, for example) that are derived across the circuit from more posterior to more anterior regions, like the ATL, in CP.

1.2. A tale of three patient groups[2]

Given the similarity in structural etiology, namely the proximity of the site of neural alteration in CP and in the other patient groups, MTL and HC, and their apparently similar functional etiology, namely a deficit in computing higher-order configurations, here, we sought to compare the behavioral profile of these three groups to evaluate whether a unique signature of perceptual impairment can be uncovered for each group. The more direct contrast is between the MTL and CP (ATL) groups, rather than against the HC group per se, but we include the HC group as a control group because any difference between the HC and MTL group allows us to localize deficits in the MTL group to regions outside the HC (i.e. to the PrC more specifically). To explore this issue, we use a series of carefully controlled experimental manipulations, obtaining data from discrimination tasks using a wide variety of stimuli.

2. Methods

2.1. Participants

Three groups of patients (MTL, HC and CP), all of who have a deficit ascribed to the more anterior/medial temporal lobe, participated in this study. Data from three different groups of control participants, matched to each of the patient groups, were also obtained. There were no significant differences in terms of age or education between each of the patient groups and their matched control groups (all $p > .05$).

MTL and HC groups and controls: The four MTL and three HC patients and their matched control participants have participated in previous studies [for example, (Barense et al., 2007; Graham et al., 2006; Lee et al., 2005; Lee and Rudebeck, 2010a)] and the data from those studies are presented here as a direct contrast with the newly acquired data from CP individuals and their controls. The MTL and HC individuals were recruited from the Memory Clinics at Addenbrooke's and Southampton General Hospitals, UK.

Structural MRI scans of the MTL and HC patients have been evaluated using qualitative visual rating methods (Barense et al., 2005b; Lee et al., 2005) and, where possible, detailed quantitative volumetrics (Barense et al., 2012b; Lee and Rudebeck, 2010a). To summarise these findings, the HC patients possessed bilateral lesions restricted to the hippocampus, with the exception of one patient who had additional, slight damage to the ATL and parahippocampal gyrus (Barense et al., 2005b). In contrast, the MTL patients possessed broader bilateral damage affecting the HC and PrC, as well as the amygdala, parahippocampal cortex, ATL, and anterior lateral temporal and fusiform cortices. Notably, imaging investigations in one of the HC and MTL patients have revealed

[2] We refer to CP individuals as 'patients' for convenience and to contrast them with the matched controls but they do not have any lesion or obvious neurological deficit.

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seemingly intact extrastriate visual areas (i.e. FFA, lateral occipital cortex (LOC) and parahippocampal place area (PPA)) and an analysis of functional connectivity of resting state networks concluded that there were no obvious findings involving posterior occipital or posterior temporal regions, which could explain their discrimination deficits (Lee and Rudebeck, 2010a; Rudebeck et al., 2013).

The sensory and basic perceptual skills of all these individuals were within normal limits, as determined by their performance on the VOSP subtests (Warrington and James, 1991). The cognitive abilities of these two groups of patients, quantified with a series of standardized neuropsychological tests, have been described in detail elsewhere (e.g., (Lee et al., 2005b)). In short, these tests revealed deficits in episodic memory and recall-based memory measures although to a differential degree in the two groups. The MTL group was more impaired on episodic and semantic memory tasks than the HC group (Lee et al., 2005). Visuospatial performance was also within the normal range for both groups (although the MTL group performed numerically more poorly than the HC group on the Benton Facial Recognition Test). The MTL but not the HC group also showed a slight semantic memory deficit. The investigation with the MTL and HC individuals received ethical approval from the Cambridge and Southampton Health Authority Local Research Ethics Committees (UK).

The MTL group comprised three patients (one female, mean age 67.7yrs; mean education 11.7yrs). Two of patients had viral encephalitis and the third suffered traumatic cerebral bleeding. Eleven elderly healthy subjects (mean age 66.4 years; mean education 12.1 years) were matched to the MTL patients.

The HC group consisted of four patients (three female; mean age 47.8yrs; mean education 15yrs). Two of the four patients had suffered from viral encephalitis, one had anoxia due to status epilepticus and one experienced carbon monoxide poisoning. Ten middle aged healthy older adults (age 47.0 years; education 13.2 years) were matched to the HC group.

CP group and controls: Six native English-speaking individuals (five females; mean age 44.5 years; mean education 14.6 years) diagnosed with CP were included in this group (Table 2). Most of these individuals, with the exception of SC, have participated in previous studies, and additional details regarding their face recognition deficits can be found in these publications (for example, (Avidan et al., 2014; Nishimura et al., 2010)). The sensory and basic perceptual skills of all these individuals were within normal limits, as determined by their performance on the VOSP subtests, although the Silhouette subtest was not included in these evaluations (Warrington and James, 1991). Twelve participants, matched individually on age, gender, and handedness served as controls for the CP individuals. All were right handed, as assessed by Edinburgh Handedness Inventory (Oldfield, 1971), except for SC and his controls (see Table 2). All participants had normal or corrected-to-normal vision and had no history of neurological or psychiatric disorder or injury. They were compensated $10 per hour. The investigation of the CP individuals and their controls was approved by the Institutional Review Board of Carnegie Mellon University.

Table 2
Demographic details and data from face recognition and handedness tests for the CP individuals. The columns containing the results of the Cambridge Face Memory Test (CFMT) and the Famous Faces test report the SDs of each CP relative to the matched controls.

Group	Initials	Sex	Age	CFMT	Famous faces	Handedness
CP	WS	F	64	−1.6	0.39	80
CP	WA	F	23	−3.5	−2.9	70
CP	KE	F	67	−1.1	−3.1	90
CP	TD	F	38	−2.2	−2.85	94
CP	SC	M	57	−1.79	−1.5	90
CP	BL	F	18	−4.16	−4.6	100

2.2. Stimuli and paradigm

Participants completed an 'oddity' task in which, on a single trial, four stimuli were displayed simultaneously and the participants were required to indicate the odd-one-out, with stimuli presented until a response was made. This experiment was run separately with five different stimulus types (Fig. 1(a)-(e). Two of the oddity tasks served as control tasks that could be solved on the basis of a single feature and were not dependent on the PrC (Barense et al., 2007; Barense et al., 2010; Lee et al., 2008): one involved size judgements (Fig. 1(a)) and the other involved low ambiguity objects (Fig. 1(b)), with the tasks designed to be as difficult as those tasks that rely on PrC function. The remaining three tasks, faces, high ambiguity objects and scenes all involved highly similar exemplars and engaged the need to discriminate between complex perceptual conjunctions. Note that the trial unique nature of the task meant that the requirement for explicit long-term memory was minimal; similarly, the influences of trans-saccadic and working memory on such tasks have been previously studied and do not seem to influence reported patterns of impairment (Erez et al., 2013; Lee and Rudebeck, 2010a, 2010b). Of note, as mentioned above, stimuli were present on the screen until response and thus any deficit we observe is not attributable to mnemonic function. We also elected not to use the same-view faces from (Lee et al., 2006a; Lee, Buckley, et al., 2005). Although matching faces presented in the same viewpoint might be solved on the basis of elemental features, observers might potentially try to solve the match based on configural information (which appears to be a default for faces; (Richler and Gauthier, 2014)) and so including this task might have confounded the interpretation of the results. Additionally, because of the relatively extensive amount of testing and time constraints, we chose the size and low ambiguity objects to be “purer” non-configural control tasks.

2.2.1. Faces (from Lee, Buckley et al., 2005)

Four images of human faces were presented for each trial (Fig. 1(c)). A set of 20 unfamiliar male faces (all Caucasian aged 20–40 years) with short hair, no facial hair or spectacles was used and each face could appear in six different views: face looking directly ahead, face upwards (head tilted back), face downwards (head titled down), face looking 45° to the left, face looking 45° to the right, face looking up and 45° to the right, face looking up and 45° to the left. On each trial, three versions of the same face identity (all in different viewpoints) appeared along with one with a different face identity (in yet a different viewpoint). Each face was presented only once in each block of trials, and across 31 trials, each face was always randomly paired with another face.

2.2.2. Scenes (from Lee, Buckley et al., 2005)

Four images of virtual reality scenes were presented for each trial on a grey background (256 levels of grey, 460 × 370 pixels (see Fig. 1(d)). A set of 62 scenes created using commercially available computer game (Deus Ex, Ion Storm L. P., Austin, TX) and a free software editor (Deus Ex Software Development Kit v112f) was used for each scene and for each of these stimuli, four different viewpoints were captured. On each trial (of 31 trials), three images of the same scene, albeit from different viewpoints, were shown with one image of a different view of another relatively similar scene.

2.2.3. High and low ambiguity familiar objects (from Barense et al., 2007)

Four images of objects common to everyday life were

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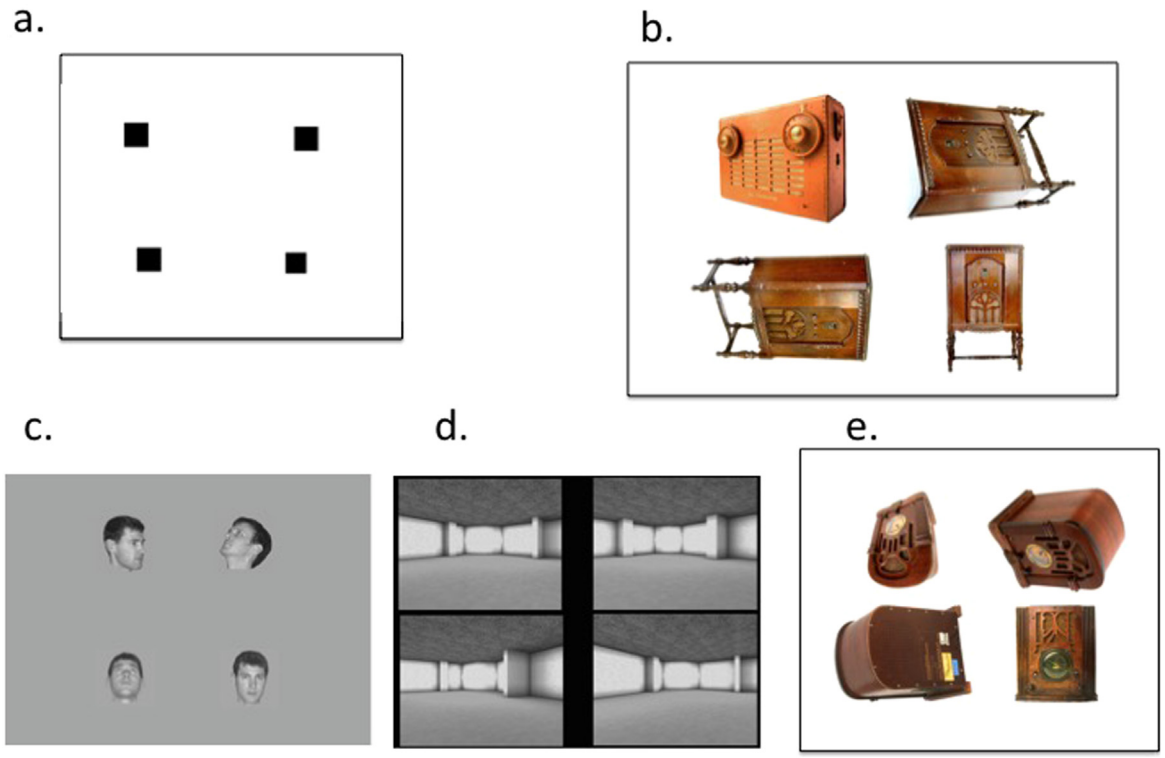

Fig. 1. Examples display of a trial from each of the five visual discriminations tasks. The first two (a: size, b: low ambiguity objects) conditions can be solved by a single feature distinction whereas the remaining three (c: face, d: scene, e: high ambiguity objects) demand a conjunction of features.

presented in each trial, and each photograph was taken from four different non-specific orientations. Objects were collected from the Hemera Photo-Objects Image Collection (Volumes 1–3) and there were two different conditions: high ambiguity and low ambiguity (Fig. 1(b) and (e)). Within a low ambiguity trial, the two objects were from the same overall category (e.g., stereos) but the two objects were easily differentiated on the basis of a single, obvious feature. By contrast, within a high ambiguity trial, the two objects shared a high number of overlapping features. Furthermore, the stimulus types were matched across the low and high ambiguity conditions (e.g., there was a high and a low trial comprised of cars, a high and a low trial comprised of stereos, etc). Trials were blocked depending on the level of ambiguity and there were 35 trials of each type.

2.2.4. Size (from Barense et al., 2007)

This task was designed to be as difficult as the high ambiguity object discrimination task but could be solved on the basis of a single feature alone and did not require the processing of complex conjunctions of object features. Four black squares were presented on each trial (see Fig. 1(a)), with three squares of identical size and the fourth either smaller or larger. The squares' positions were jittered slightly so that the edges did not line up along vertical or horizontal planes. The length of each side was randomly varied from 6 to 247 pixels. The size difference varied between 9 and 15 pixels and the size of each square was trial-unique. On each trial of 35 trials, either three identical smaller squares were shown with one larger square or three identical larger squares were shown with one smaller square.

2.2.5. Procedure

The experiments were programmed using E-Prime software (Psychology Software Tools Inc., Pittsburgh, PA). Practice trials were administered first and feedback was provided.

All tasks were based on an oddity paradigm in which the participants were instructed to select the "odd-one-out" from an array of simultaneously presented stimuli as quickly and as accurately as possible (Barense et al., 2007; Buckley et al., 2001; Lee, Buckley, et al., 2005). In all tasks, participants viewed a display consisting of four items in two rows of two, with one of the four stimuli differing from the others. On each trial, the position of the odd-one-out was randomized.

During the experiment, no feedback was given. Both accuracy and response time were recorded.

2.2.5.1. MTL, HC and their controls. The patients were tested in their own homes, and control subjects were tested at the MRC Cognition and Brain Sciences Unit by Barense and/or Lee. All tests were computerized tasks and were conducted on a 15 inch SVGAL CD touchscreen at 1024×768 resolution. A single trial was displayed on a computer screen. During the test, the response consisted of touching any item, which resulted in the offset of the stimulus display and the onset of the next trial. The face and scene conditions were completed approximately 3 years before the object and size conditions, with the different conditions within each session counterbalanced across participants.

2.2.5.2. CP and their controls. All individuals were tested at Carnegie Mellon University and run on a laptop Dell Latitude E6430 with a 14 in. screen. Responses were collected by participants' clicking a mouse over the odd stimulus. The computer screen was split into four quarters, and a correct response was recorded when a subject clicked anywhere in the quarter that contained the correct response. This resulted in the offset of the stimulus display and the onset of the next trial. The five conditions were completed in one session and the order was counterbalanced across participants.

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3. Results

The results section is broken down into two major sections. The first set of analyses compares the performance of the patients relative to their own control groups. This analysis is important as the control groups were designed to be matched specifically to each of the patient samples. Furthermore, because there were some differences in the acquisition of the data (for example, the MTL and HCs and their controls responded via touch screen, and the CPs and their controls via mouse), a direct comparison of patients and controls under the same acquisition scenario is critical. The patient groups were compared to their matched controls on accuracy of performance as well as on reaction time (RT). Also, because individuals with CP have been shown to trade speed against accuracy (Behrmann et al., 2005a), we also analysed performance in terms of inverse efficiency (IE). Inverse efficiency is equal to the mean RT divided by the proportion of correct responses, calculated separately for each condition and each participant. Lower values on this measure indicate better performance (Akhtar and Enns, 1989; Townsend and Ashby, 1983). Note that because our primary interest is in the interactions between group x condition (i.e., whether there were differences between patients and controls on particular oddity tasks), we focus on the interactions primarily. We report main effects of group where they exist but do not report differences across conditions (it is unsurprising if performance on the low ambiguity object task is easier than the other tasks, for example). The second set of analyses directly pits the three groups of patients against each other using z-scores. By using z-scores and deriving the deviation in performance relative to the appropriately matched control mean, we are equating the comparison across the three patient groups and controlling for the differences in data acquisition.[3]

3.1. Patients groups versus tailored control groups

Because the accuracy findings from the MTL and HC groups have been reported previously (Barense et al., 2007; Lee, Buckley et al., 2005), we start with these two groups and essentially duplicate these published findings. New to this paper, we analysed the RT data obtained in these patients. For each group, a repeated measures Analysis of Variance (ANOVA) was conducted with group (patients vs. controls) as a between-subjects factor and task (faces, scenes, high object, low object, size) as a within-subjects factor.

3.1.1. MTL group versus controls

As confirmation of the previous findings (see Fig. 2), there was a significant group x condition interaction for the MTL analysis with accuracy as the dependent measure, ($F4, 40 = 4.6$, $p < .004$), and pairwise *t*-tests (all at $p < .05$) revealed that the MTL group performed significantly less accurately than the matched controls for face, scene and high ambiguity objects, but not for low ambiguity objects or size. The MTL group's accuracy was also higher on the low ambiguity and size conditions than on any of the other three oddity tasks ($p < .01$ for pairwise comparisons). Unsurprisingly, the MTL group were less accurate overall than the controls, [Group ($F1,10 = 50.2$, $p < .000$)]. The same ANOVA with RT or with IE as the dependent measure revealed no significant differences between the MTL and control groups (RT: condition x group ($F4,40) = .265$, $p > .8$); IE: condition x group ($F4,40) = 1.54$, $p > .2$)). Even though some of the pairwise comparisons on IE appear to differ, this is unsurprising given the accuracy differences and so we do not focus on these findings any further.

3.1.2. HC versus control group

The same ANOVA performed on the accuracy data from the HC group and their controls also revealed a significant interaction of group x condition ($F4, 36 = 4.6$, $p < .04$) (see Fig. 3(a)). Pairwise *t*-tests revealed a significant difference between the groups only on the scene oddity task, and the HC group's performance on the scene task was also significantly poorer than the accuracy on any of the other tasks (pairwise *t*-tests $p < .01$). Overall, the HC group performed more poorly than their matched controls, [Group ($F1,9 = 7.4$, $p < .04$)].

There were also significant interactions between group x condition in RT, ($F(4,36) = 2.6$, $p = .048$) (see Fig. 3(b)), and in IE, ($F(4,36) = 4.4$, $p = .005$) (see Fig. 3(c)). Based on posthoc *t*-tests (Bonferroni correction, $p < .01$), in RT, the HC group performed more slowly than their controls on scenes and on faces. In IE, performance was poor relative to the controls only on the scene task (Bonferroni correction, $p < .01$), and, performance on the scene task was significantly poorer than their performance on the other tasks.

3.1.3. CP versus controls

The ANOVA with accuracy as the dependent measure and the CP group and controls revealed a group x condition interaction, [($F4, 60 = 3.9$, $p < .007$)], although no main effect of group was observed ($F > 1$) (see Fig. 4(a)). As revealed by posthoc *t*-tests (Bonferroni correction $p < .01$), the CP group was significantly less accurate than the controls in face discrimination.

There was also a significant interaction between group x condition in RT, ($F4, 60 = 3.2$, $p < .02$), as well as a main effect of group ($F1, 15 = 6.1$, $p = .03$) (see Fig. 4(b)). Pairwise *t*-tests (again $p < .01$) revealed significantly slower performance on faces and scenes, with a similar trend for high ambiguity objects, and, within the CP group, RT was significantly slowed on all three conditions, albeit to a greater degree for faces and scenes, compared with low ambiguity objects and size. Finally, the same ANOVA but with IE as the dependent measure also revealed a group x condition interaction ($F4, 60 = 4.2$, $p < .005$), as well as a main effect of group ($F1, 15 = 5.7$, $p = .03$). As evident in Fig. 4(c), the CPs performed significantly more poorly than their controls on face and scene oddity and marginally more poorly ($p = .08$) on high object ambiguity oddity, as well.

3.1.4. Single subject data

Because the groups are small and the data from a single individual carries substantial weight in the analysis, we also examined the data from every patient individually. To this end, we adopted the single-case statistical method (Crawford and Garthwaite, 2004) and compared each individual patient's score against the matched control group mean and SD on accuracy (see Fig. 5).

For the MTL group, all individuals scored outside the normal range of performance on the face task and 60% of them did so for scenes and for high ambiguity objects (and a third individual's data was marginally significant at $p = .08$), as well. One third of the group scored significantly outside the normal range on the size oddity task. Of the HC individuals, 75% of the group scored abnormally on scenes and half the group was marginally out of the normal range on low ambiguity objects. Last, 75% of the CPs scored outside the normal range on faces (and this was true when IE was used, as well) and 30% were outside the normal range on scene, high object and low object conditions, as well.

These findings characterize the object discrimination difficulties across the three groups of patients. Although the findings are

[3] One of the CP individuals (KE) did not complete the low ambiguity task and one HC, EB, did not complete high or low ambiguity objects or size. For these individuals, we have inserted the mean of the sample into the empty cell to facilitate the analyses but this does not change the mean of the group.

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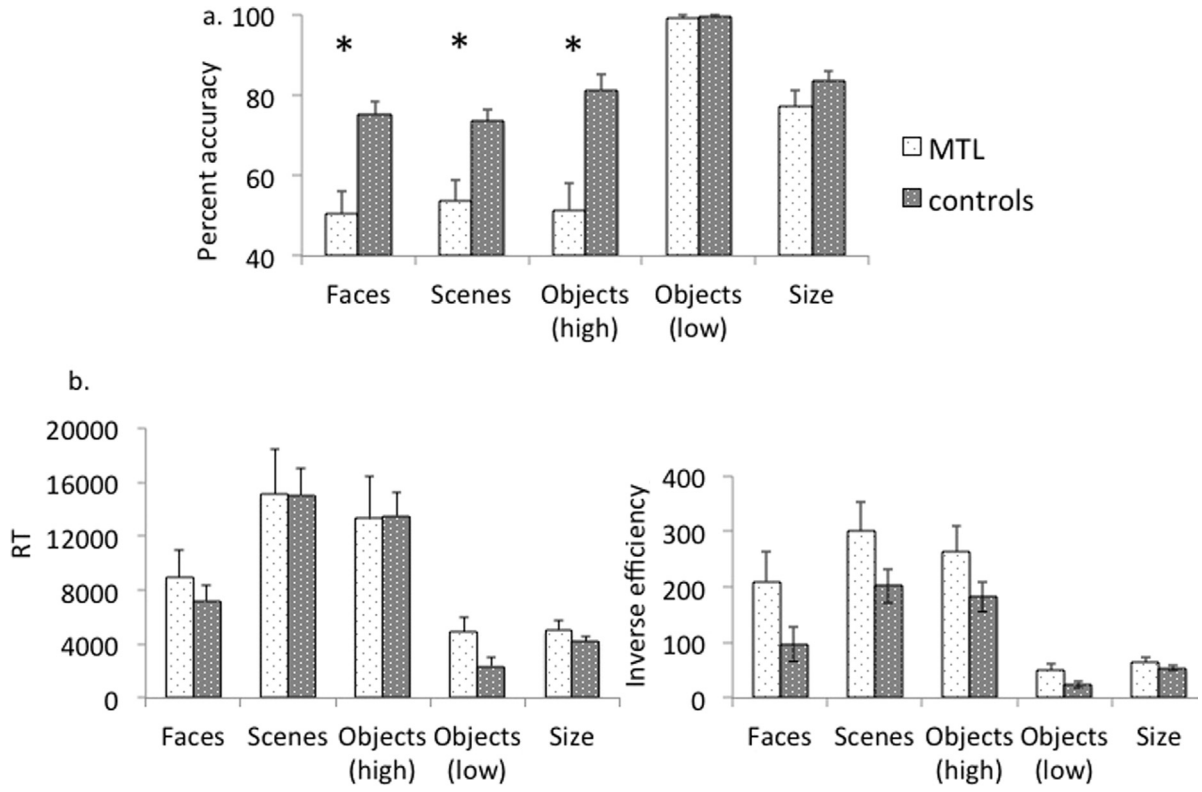

Fig. 2. Comparison of MTL and control group. Mean percent accuracy (and 1 SE) for the MTL group and their control group across all five discrimination conditions. * signifies significant differences between groups. There were no differences between the MTL and control groups on RT or IE and so we do not display those data.

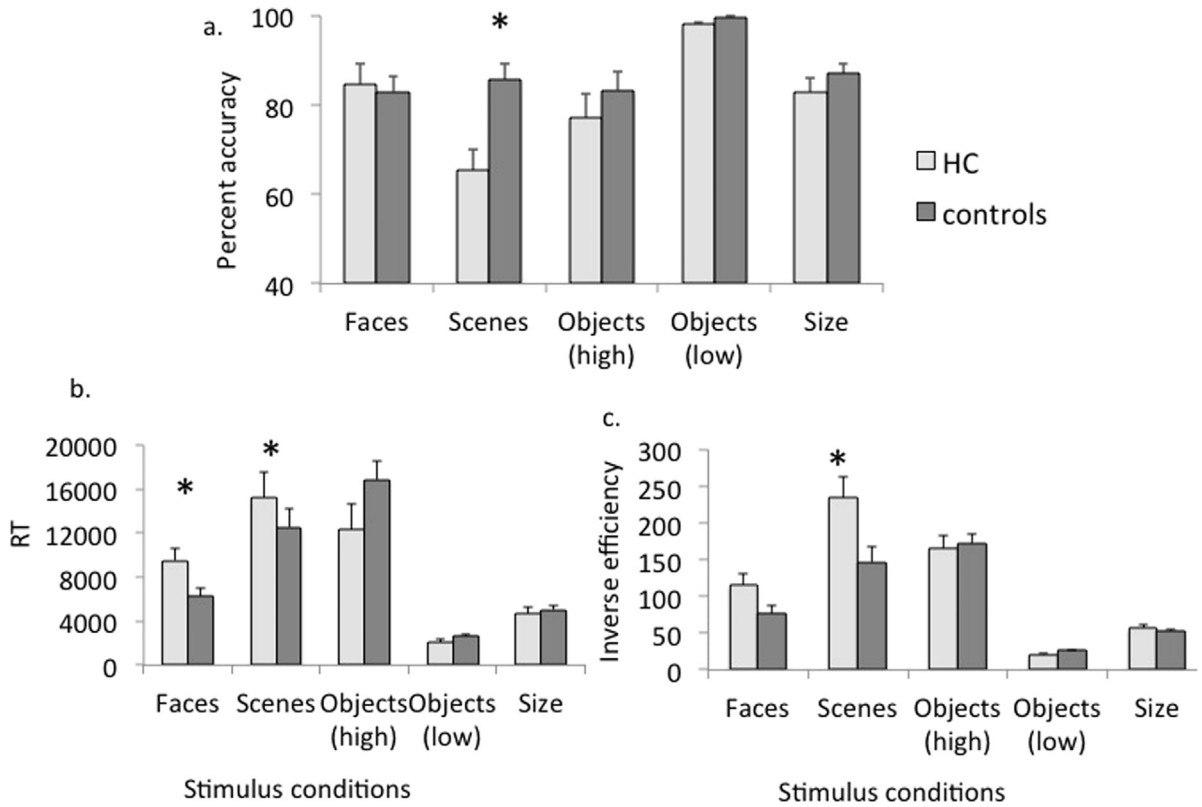

Fig. 3. Comparison of HC and control group. a. Performance of HC group and their control group across all five discrimination conditions as reflected in (a) Mean percent accuracy (and 1 SE), (b) Mean RT (and 1 SE), and (c) Mean Inverse efficiency (and 1 SE). * signifies significant differences between groups.

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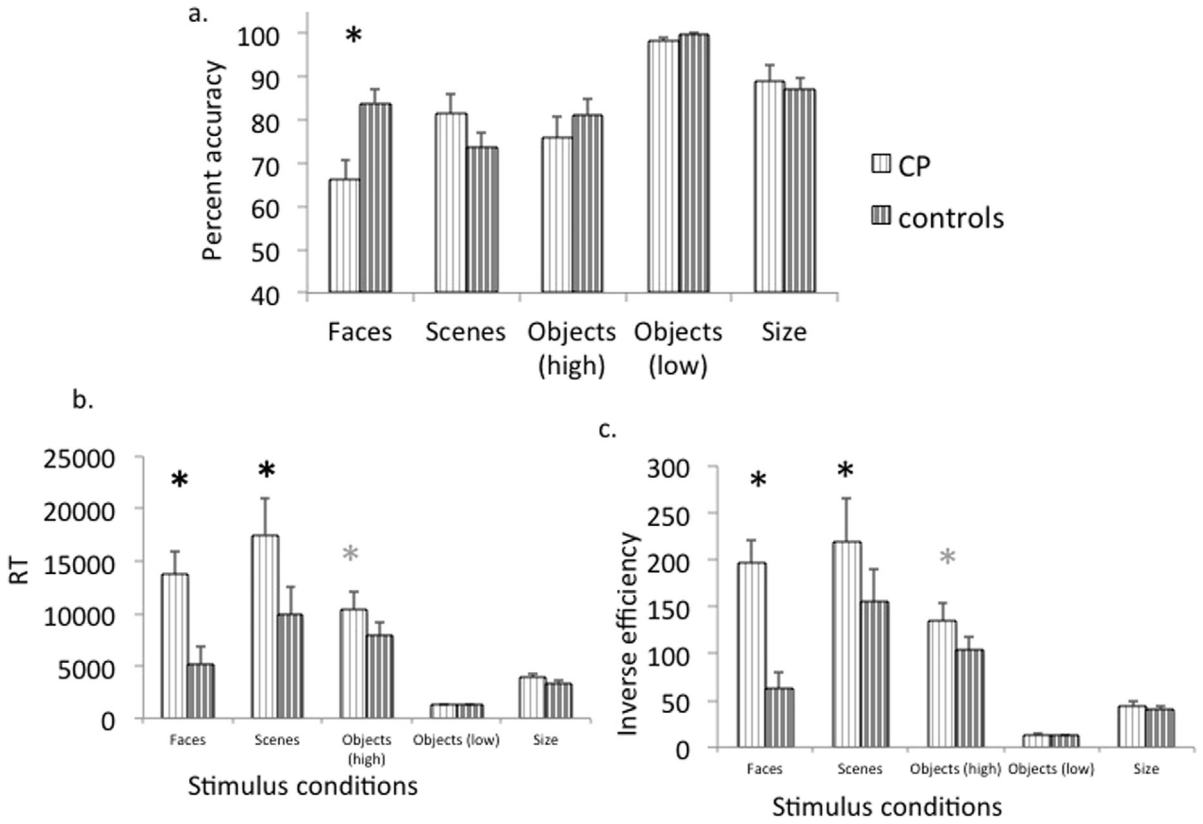

Fig. 4. Comparison of CP and control group. a. Performance of CP group and their control group across all five discrimination conditions as reflected in (a) Mean percent accuracy (and 1 SE), (b) Mean RT (and 1 SE), and (c) Mean Inverse efficiency (and 1 SE). * signifies significant differences between groups.

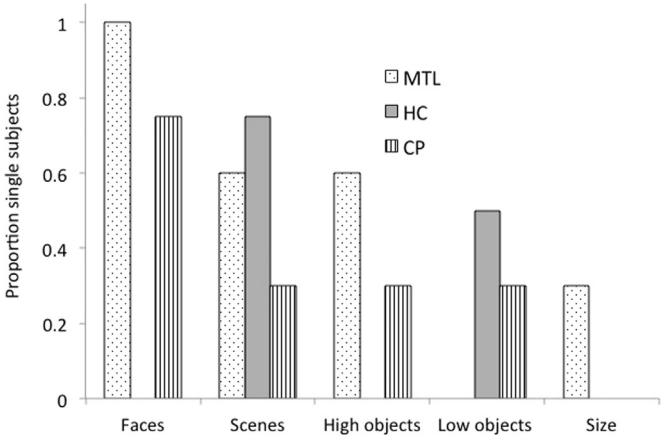

Fig. 5. Single subject data. Percentage of individual participants from the MTL, HC and CP group who fell outside the normal distribution on each experimental condition.

not absolutely identical across all dependent measures, there is sufficient consistency to reveal that the profile of each group, relative to matched controls, is slightly different. Whereas both the MTL and CP groups discriminate faces, scenes, and high ambiguity objects poorly (although the last task/s to a relatively lesser extent in CP than in MTL and evident primarily in RT and IE), the HC group shows impaired discrimination primarily on scenes. The question now is whether, when pitted against each other, the groups (especially the MTL and the CP groups) differ.

3.2. Direct comparison of three patient groups

Because there were some differences in the way the data were acquired for each group and there are obvious differences in the composition of the three groups in biographic factors as well (e.g., age, handedness, and gender), a direct comparison of the three patient groups seems inappropriate. To establish a more equitable means of comparison, we compared the data across the three groups using z-scores computed first on the basis of the accuracy data. For each participant for each condition, we first calculated the accuracy z-score relative to the matched control group. We then used the z-score in the repeated measures ANOVA with group (MTL, HC, CP) as the between-subject factor and condition as the within-subjects factor. The rationale for this approach is that the normalized scores will serve as a more legitimate way of comparing the groups to each other rather than using the absolute dependent measures.

Fig. 6 plots the average z-score for each group in accuracy. The results of the ANOVA on these data revealed a significant interaction of group x condition, ($F(8, 40 = 3.2$, $p < .007$). There were neither a main effect of group nor of condition, providing reassurance that the group comparison was conducted with other variables equated. We then conducted pairwise *t*-tests across the groups for each condition and report here only those comparisons that exceeded $p < .01$. The analysis yielded the following results: the CP and MTL groups did not differ on the face, low ambiguity or size oddity tasks, but for scenes and for high object ambiguity, the CP group z-score was significantly more positive than that of the MTL group. The CP and HC groups did not differ on high ambiguity objects, low ambiguity objects or size but the CPs z-scores were significantly more negative than those of the HC for face oddity but significantly more positive for scene oddity. Last, the MTL group had significantly more negative z-scores than the HC group for faces and high ambiguity objects but performed as poorly as the HC group on scene oddity. The two groups performed equally well on low ambiguity objects and size (both groups scores do not

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Fig. 6. Comparison of MTL, HC and CP groups using accuracy. Mean accuracy z-scores (and 1 SE) for the CP, MTL and HC groups across all five discrimination conditions. A negative z-score indicates impairment.* signifies significant differences between groups.

differ from zero).

RT was not as informative as accuracy (for example, in the MTL group), but we nevertheless compared the three groups to each other using the z-scores in RT computed for each participant and for each condition.[4] Although the interaction of group x condition, ($F(8,40)$=n. s.), was not significant, we nevertheless explored some of the pairwise comparisons especially between the two key groups, the CP and MTL patients. The only significant difference was the z-scores for faces with the CP group showing more positive (i.e. longer RTs for CP relative to own control group) scores than the MTL group relative to their control group. There was a trend for this same effect for scenes but it did not reach significance and no other differences reached significance.

3.3. Summary of analyses

In summary, we conducted two analyses, one of which reveals the perceptual strengths and weaknesses of each of the three patient groups, the MTL, HC and CP, against their matched controls, and the second of which compares the patient groups against each other, having normalized their scores relative to their matched control groups. In the first set of analyses, although the profiles of the patients differed slightly statistically depending on the dependent measure used, the overall findings demonstrated that the MTL group performed more poorly than the controls on faces, scenes and high ambiguity objects. The HC group performed more poorly than the controls predominantly on scenes and to a lesser extent on faces (in RT, slower than matched controls). Last, the CP group performed more poorly than controls on faces and to a lesser extent on scenes and marginally so on high ambiguity objects. Note that no patient group differed from the controls on either the low ambiguity or size condition, revealing that the impairments exhibited were always to those tasks that relied on more complex perceptual demands. Importantly, however, even when perceptual difficulty was increased, as in the size oddity task, this alone did not suffice to elicit impairments in the patient groups. Thus, the key dimension separating tasks that do and do not reveal impairment is assumed to be the requirement for configural processing when featural differences (even if subtle and demanding) do not suffice for the discrimination. The abnormal patterns of the MTL and HC groups have been described previously (albeit not for all dependent measures reported here) and so the novel finding here is that the CP group are impaired on similar tasks to individuals with amnesia from MTL damage, and although their perceptual discrimination performance is fairly widely affected (faces, scenes, high ambiguity), performance is especially poor for the CP for faces relative to the level of impairment seen in the other conditions. These findings are largely mirrored in the analysis of the single subject data.

The analysis of the z-scores using the accuracy data brings the difference between the three patient groups into sharp relief and highlights the differential perceptual signatures across the groups (see Fig. 6). The HC group stands out for its specific difficulty in discriminating scenes and the CP group stands out for its specific difficulty in discriminating faces. The MTL group, in contrast, evinces a more general discrimination deficit, performing as badly as the HC on scenes, as badly as the CP on faces, and more poorly than either of the other two groups on high object ambiguity oddity. The groups did not differ on their normalized accuracy for the low ambiguity objects or for the size discrimination, which was notably matched for difficulty with the more complex high ambiguity perceptual conditions. The analysis of the z-score on RT provides a slightly different account: CPs continue to be poorest at faces (slowest RT) and trend towards slowing on scenes and high objects too, but no other RT z-score reveals a significant difference across groups. (Fig. 7).

4. Discussion

There has been growing recognition from studies of human and non-human primates that structures in the medial temporal lobe (MTL) contribute to processes beyond memory (Graham et al., 2010; Moscovitch et al., 2016; Murray et al., 2007; Nadel and Peterson, 2013). Previous studies that have focused on the contribution of the MTL to perceptual function, for example, have acquired data from patients with hippocampal (HC) or medial temporal lobe (MTL) lesions and have provided strong evidence to support this hypothesis: HC damage leads to an impairment in perceiving (but also learning and remembering) complex scenes whereas MTL damage, which affects both the HC and the PrC, results in perceptual and mnemonic deficits for scenes but also for faces and for objects (Barense et al., 2005a, 2010, 2012b; Graham et al., 2010, 2006; Lee et al., 2005a). Importantly, all of these patients are able to discriminate objects that differ on a simple feature, such as size, even when the discrimination is taxing, ruling out a basic sensory or low-level visual impairment. This result has

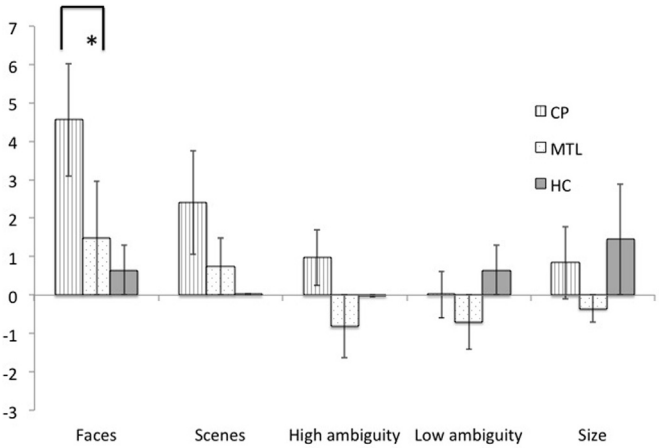

Fig. 7. Comparison of MTL, HC and CP groups using RT. Mean RT z-scores (and 1 SE) for the CP, MTL and HC groups across all five discrimination conditions. A positive z-score indicates impairment. * signifies significant differences between groups.

[4] One of the three MTL participants had an RT that exceeded 3 SDs of the other 2 individuals, resulting in a skewed group mean. For this analysis, we assigned the mean of the other 2 individuals to this third individual (winsorized) but interpret this result with caution.

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been further substantiated by studies using fMRI (Barense et al., 2010; Lee et al., 2008; Mundy et al., 2013), which revealed differential recruitment of the HC and MTL/PrC for scene and face discriminations, respectively. Consistent with this, macaque monkeys with lesions to PrC are impaired at visual discrimination tasks when presented with arrays of similar faces and similar objects (Buckley et al., 2001; Buckley, Charles, Browning, and Gaffan, 2004; Buckley and Gaffan, 1998). All of these findings are compatible with a theoretical account in which, as one moves more rostral in the ventral visual cortex, structures are increasingly engaged in deriving complex conjunctions of features that ultimately uniquely depict a specific exemplar and allow for its differentiation from other similar exemplars.

Interestingly, in recent years, albeit in an independent domain of investigation, a similar anatomical and functional explanation has been offered to account for the face recognition impairment in individuals with congenital prosopagnosia (CP) (Avidan and Behrmann, 2014; Stollhoff et al., 2011b). The central claim is that the disconnection between more posterior visual regions (e.g. FFA and OFA) and more anterior regions such as the anterior temporal lobe results in a deficit in face individuation and that this deficit may well be a consequence of an impairment in deriving more holistic or configural representations. While this computational ability is critical for faces, all of which share the same basic elements arranged in the same spatial configuration, discriminating between homogeneous within-class exemplars in other categories may be affected as well.

In light of this apparent overlap between these disparate neuropsychological populations both in anatomy of the lesion and the functional etiology of the deficit, we directly compared the performance of MTL and HC patients, on the one hand, and CP individuals, on the other, using a set of tasks that do or do not require the conjunctive binding of features. The key findings were as follows: whereas the HC patients were disproportionately impaired in discriminating scenes (although RT for face discrimination was significantly slowed too) and the CP individuals were disproportionately impaired in discriminating faces (although deficits in scene and high ambiguity objects were also present in RT and inverse efficiency measures), the MTL patients were impaired on all three classes that stressed feature conjunctions and this was to roughly an equivalent degree across these three classes. All groups performed normally, relative to their matched controls, when discriminations could be completed on the basis of a more simplistic featural difference even when the task itself was challenging (size and low ambiguity objects). The group results were largely mirrored in the analysis of the data from each individual patient, relative to the distribution of the control group, and roughly the same findings were reflected in the analysis of the z-score data (mostly in accuracy comparisons).

As evident from this summary, the scope of the recognition deficit in both the MTL and CP groups extends beyond face processing. Although this may not be that surprising in the MTL cases given their extensive deficit, this may, perhaps, be more surprising in the CP cases. Whether individuals with CP are impaired on recognition of any other stimulus classes has been the topic of ongoing debate, with some studies reporting face-specific deficits and others uncovering more extensive impairments. To evaluate this issue more closely, Geskin and Behrmann (under review) undertook a survey of roughly 114 published papers on 672 cases of CP from 1976 to the current time by searching for 'prosopagnosia' on Pubmed and then narrowing the results down to those cases without acquired lesions either early or later in life. Then, as far as possible, the profile of each CP individual was assessed to discover whether there is statistically normal non-face recognition along with a statistically significant impairment in face recognition (roughly akin to the analysis done on acquired forms of agnosia; (Farah, 1991). If all dependent measures are taken into account (i.e. not only accuracy but also RT and even inverse efficiency to account for the speed-accuracy trade-offs), there appear to be very few cases, if any (for whom sufficient data was available for analysis), in the existing literature who have normal object recognition and in some of these instances, there is still not quite enough information to make the judgment definitively. In all cases, the impairment in face recognition was more severe than that for other non-face stimuli (e.g. objects such as cars or Greebles) but many explanations for this asymmetry have been offered including the homogeneity among face exemplars and the heavy reliance on configural processing (for example, (Gauthier et al., 1999). The findings from the present study are compatible with the findings from the literature in that the CP individuals, for the most part, reveal deficits in scene and object discrimination, albeit to a lesser degree than the difficulties in face perception.

A number of important conclusions can be drawn from the results of the current investigation, with respect to the overlap in the neural pattern and the overlap in the functional deficit (configural coding). First, there is a marked likeness in the face performance profile in MTL and CP, suggestive of a similarity in the underlying neural basis of the deficits. The MTL individuals have sustained clear neurological damage (viral encephalitis or bleed secondary to trauma) that has resulted in a lesion to the MTL region, including the PrC and more anterior ATL structures such as the temporal pole. The 'deficit' in the ATL in the CP case is, on some accounts (e.g. (Avidan et al., 2014)), a result of a disconnection between more posterior and more anterior face-selective regions including the ATL but perhaps including the PrC, as well. The question is whether the same neural structures are affected in both of these populations, albeit as a result of different etiologies. As we have indicated, some of the regions classified as "ATL" might well have been classified as "PrC" had another group been doing the labeling (see Table 1 for overlap in coordinates), reflecting the ambiguity in localizing the source of the deficit.

Further support for the possibility that the same region/s might be implicated in the patient groups comes from more direct fMRI studies of face perception in which the documented foci of activity observed in ATL face-sensitive regions may include PrC as well (Harry, Umla-Runge, Lawrence, Graham, and Downing, 2016). This is well illustrated by O'Neil et al., (2013) who directly compared activity for a face oddity task similar to the one used in the current study with activity driven by a classic face localizer scan, and reported overlap in a region that was confirmed to be in right PrC (defined based on boundaries provided by (Pruessner et al., 2002)). More recent MVPA-based fMRI work from this same group has shown that face specific responses in PrC (again confirmed based on criteria in Pruessner et al., 2002) are also present in distributed patterns that extend beyond the 'blob' that typically shows up in univariate analyses of functional localizer data or data from recognition memory tasks for faces (Martin, Cowell, Gribble, Wright, and Kohler, 2015), implicating a slightly larger region that might be affected in both MTL and CP groups.

Several explanations may account for the overlap in neural correlates for the MTL and CP individuals. One possibility is that a large swath of cortex is activated in response to faces and that there is insufficient precision in delineating the different ROIs. Imprecision resulting from a reduction in signal precision in functional imaging of the key areas is indeed of relevance here and signal drop-out and distortion in the inferior and medial surface as well as the polar tip of the ATL are common and especially problematic when studies use a high TE and large voxel size. Thus, the signal may not be sufficiently precise to segregate the discrete functional subregions of ventral ATL (Ding et al., 2009; Wong and Gallate, 2012). FMRI studies in non-human primates have identified somewhat variable activation loci for faces, varying from the

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inferior bank of the STS on the lateral surface to the inferior surface of the ATL (Ku et al., 2011). In humans, MVPA studies of facial identity using novel faces have also reported somewhat different loci in the right ventral ATL: some studies have reported an extremely medial peak in the uncus, possibly corresponding to perirhinal cortex (Nestor et al., 2011; Von Der Heide et al., 2013) whereas in others, the activation is more closely associated with the right ventral ATL (Kriegeskorte et al., 2007). But the activation profile may also be somewhat contingent on the particular contrast. For example, in Von Der Heide et al., (2013), the activation to novel faces was most similar to Nestor et al., (2011) while the activation to familiar minus novel faces were in a similar depth plane to that reported by Kriegeskorte (2007), but slightly more anterior (famous vs. novel faces: −32, 14, −36; best friends vs. novel faces: −47, 11, −31). Last, the activation for the contrast of famous faces minus novel landmarks on the surface of the ATL was centered at left (−36, 6, −42) and right (35, 3, −42) locations (Von Der Heide et al., 2013).

Further advances in developing more fine-grained distinctions between anterior/medial temporal lobe structures will likely come from two separate approaches. One approach will address the limitations outlined above, resulting in increased precision in delineating the ROIs and acquiring better imaging acquisition protocols that offset the drop-out and artifact of scanning these anterior regions. A second avenue of progress will come from improved parcellation of the temporal pole and surrounding regions with modern neuroanatomical techniques, combined with different cellular, neurochemical, and pathological markers. Such investigations find that at least six different areas extend into the ATL, with another area being unique to the polar region (Ding et al., 2009). As noted by Ding et al., (2009), the classic anatomical concept of treating the human temporal pole as a single area (area 38) is clearly inadequate and needs re-evaluation: the classic studies on human cortical mapping were mainly based on Nissl preparations but close exploration reveals that this part of cortex is a large, heterogeneous area containing cytoarchitectonically distinct regions (Bonner and Price, 2013). Additional progress is being made through studies of white matter connectivity to these temporal regions and through evaluating the relationship between the fiber tracts and behavior as well as between the white matter tracts and functional activation profiles. For example, in one study combining measurements of white matter structure, functional selectivity and behavior in the same subjects, two parallel white matter tracts were uncovered, one connecting to face- and one to place-selective regions and the diffusion properties correlated with behavioral profile for face or place processing (Gomez et al., 2015). Even more pertinent are the findings from recent studies of the contribution of the inferior longitudinal fasciculus, ILF, and the fornix in perceptual discrimination tasks similar to those used here (Hodgetts et al., 2015; Postans et al., 2014). Microstructure of the fornix, a principal tract linking the HC with adjacent cortical and subcortical structures, was correlated with perceptual discriminations of scenes but not faces, and, conversely, microstructure of the ILF, the main ventral pathway to the anterior temporal lobe was correlated with perceptual discriminations of faces but not of scenes. Moreover, the integrity of these pathways was associated with the BOLD response, with the ILF associated with the functional response for faces in FFA and also in the PrC (see also (Pyles et al., 2013)) and fractional anisotropy measures of the fornix were positively associated with HC scene de-activations. Together, these findings segregate the connectivity of the more anterior/medial temporal structures and show that these anatomical connections comprise broader networks that are dissociable in the types of stimulus representations they support. Moreover, it appears that these different regions can be dissociated (to some extent) by discrete damage. Together, the data support the claim that visual discriminations are subserved by neurocognitive networks associated with critical anterior/medial temporal lobe structures and that examining the interplay between cortical functions, anatomical connectivity, visual behaviors and the effect of selective brain damage offers insight into the nature of these widely distributed networks and their role in visual perception.

Last, in addition to increasing precision in the empirical domain, increasing precision in the computational characterization of the instantiated function is needed too. That these anterior/medial regions all appear to play a role in deriving conjunctions of features is a rather coarse description of the functional role played by these regions in perception and memory. Also, whether similar conjunction or binding functions affect other category-sensitive regions distributed throughout the temporal and occipital lobe remains to be determined. Increasing specificity, theoretical consideration and perhaps simulations of the imputed contributions would further our understanding of this region of cortex, as well as the way in which representations may differentially support success on perceptual and mnemonic tasks.

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