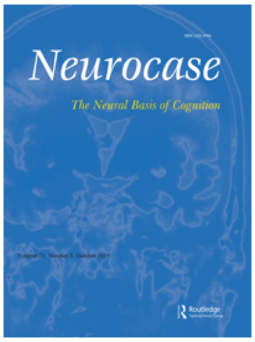

Neurocase

The Neural Basis of Cognition

ISSN: 1355-4794 (Print) 1465-3656 (Online) Journal homepage: http://www.tandfonline.com/loi/nncs20

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To cite this article: Ingrid R. Olson, Youssef Ezzyat, Alan Plotzker & Anjan Chatterjee (2015) The end point of the ventral visual stream: face and non-face perceptual deficits following unilateral anterior temporal lobe damage, Neurocase, 21:5, 554-562, DOI: 10.1080/13554794.2014.959025

To link to this article: http://dx.doi.org/10.1080/13554794.2014.959025

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Neurocase, 2015
Vol. 21, No. 5, 554–562, http://dx.doi.org/10.1080/13554794.2014.959025

The end point of the ventral visual stream: face and non-face perceptual deficits following unilateral anterior temporal lobe damage

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(*Received 13 August 2013; accepted 19 August 2014*)

While it has been claimed that the ventral visual stream ends in the inferior aspects of the anterior temporal lobe (ATL), little is known about whether this region is important for visual perception. Here the performance of two patients with unilateral ATL damage was assessed across four visual perception tasks that parametrically varied stimulus similarity. Patients performed normally on difficult judgments of circle size or face age but were impaired on face identity and dot pattern matching tasks. Portions of the ATL, most likely the ventral surface, may have a functional role in visual perception tasks requiring detailed configural processing, most commonly used to discern facial identity.

Keywords: face perception; prosopagnosia; perirhinal cortex; temporal pole

The anterior temporal lobe (ATL) consists of the temporal pole (BA 38), anterior aspects of the superior, middle, and inferior temporal gyri, as well as anterior aspects of the entorhinal cortex (BA 28 and 34), and anterior aspects of the perirhinal cortex (PRC) (BA 35 and 36). The ventral ATL (vATL) receives input from more posterior visual areas whereas the dorsal ATL receives input from tertiary auditory areas (Kondo, Saleem, & Price, 2003, 2005; Nakamura & Kubota, 1996). Likewise, visual stimuli, regardless of task, tend to activate ventral portions of the ATL while auditory stimuli, regardless of task, tend to activate dorsal portions of the ATL (Olson, Plotzker, & Ezzyat, 2007). Thus, the end point of the ventral visual stream is thought to be in ventral aspects of the ATL (Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013).

Research on this topic has focused on a subregion of the ATL, the PRC, which appears to play some role in higher order perception (Buckley, Booth, Rolls, & Gaffan, 2001; Bussey & Saksida, 2002; Murray & Bussey, 1999). Various studies have reported that monkeys with focal PRC lesions cannot find the "odd" stimulus from a group of six simultaneously displayed items, and that the level of impairment varies according to the degree of feature ambiguity or feature overlap present in the stimuli (reviewed in Buckley & Gaffan, 2006; Bussey, Saksida, & Murray, 2006). Similarly, humans with large medial temporal lobe (MTL) lesions that include PRC perform normally on perception tasks that require the comparison of simple features such as color or size. However, when the task can only be solved by comparing feature complexes, performance breaks down (Barense et al., 2005; Lee, Barense, & Graham, 2005; Lee, Buckley, et al., 2005; Lee, Bussey, et al., 2005; Lee et al., 2006).

Discerning facial identity relies heavily on comparing feature complexes. A small but growing number of neuroimaging studies have reported that portions of the vATL are sensitive to face processing. In univariate functional magnetic resonance imaging (fMRI) studies, viewing famous faces is consistently associated with bilateral ATL activations. In addition, multivariate fMRI studies have reported that a small region in the vATL, in PRC, is more sensitive to individual facial identities than other regions of the face network (reviewed in Von der Heide, Skipper, & Olson, 2013). Although it is tempting to view these findings as indicating a role of the vATL in face identity processing, findings from neuropsychology suggest that the role of this region in face processing might be best characterized as mnemonic. Humans with ATL damage consistently exhibit problems with person memory, a disorder that Damasio, Tranel, and Damasio (1990) termed "amnesic associative prosopagnosia." Focal unilateral lesions of the ATL due to stroke, insult, or resection surgery have difficulties remembering information about people, especially their names (reviewed by Olson et al., 2007). Damasio et al. (1990) did extensive research on the face processing capabilities of these individuals and reported that while face perception was intact, face memory was impaired.

Indeed, the greater ATL has historically been associated with mnemonic processing. Some investigators hypothesize that the ATLs have semantic memory

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This article was originally published with errors. This version has been amended. Please see Corrigendum (http://dx.doi.org/10.1080/13554794.2014.972725).

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functions (Graham, Simons, Pratt, Patterson, & Hodges, 2000; Patterson, 2007) while the entorhinal cortex and PRC have been associated with declarative memory formation as part of the greater MTL memory system (Squire & Zola-Morgan, 1991). Yet hints that the ATL is involved in visual discrimination go back many decades. It has been reported that patients with right ATL damage cannot accurately report how many dots were present in a rapidly shown dot configuration (Kimura, 1963), cannot accurately find the odd circle out of a set of four fragmented circles (Meier & French, 1965), and cannot accurately sort schematic black and white faces called "Mooney faces" into categorical piles (Lansdell, 1968).

Findings linking PRC to high-level perceptual processing are controversial, however. Some groups have not observed perceptual deficits in monkeys or humans with PRC damage (Buffalo, Reber, & Squire, 1998; Hampton, 2005; Holdstock, Gutnikov, Gaffan, & Mayes, 2000; Levy, Shrager, & Squire, 2005; Stark & Squire, 2000). In addition, the possibility of a latent memory component exists in some perception tasks. Perceptual deficits in humans and monkeys with PRC damage are typically observed when a large array of similar stimuli must be discriminated, raising the question of whether memory for the previously fixated objects is impaired. Last, it is difficult to attribute the results of the human lesion studies specifically to the PRC. Damage to this area always accompanies damage to other temporal lobe structures. In the studies by Graham and colleagues (Barense et al., 2005; Lee, Barense, et al., 2005; Lee, Buckley, et al., 2005; Lee et al., 2006), the perirhinal patients had extensive medial and ATL lesions that potentially contributed to the observed deficits.

The purpose of this study is to help clarify the role of the ATL in high-level perception generally, face perception more specifically. We tested two patients with lesions that damaged the ATL but spared the hippocampus and the posterior parahippocampus. Patients did not self-report any episodic memory problems, nor did they show any memory impairments when tested more formally. We further minimized the possibility that impaired memory performance could contaminate performance on a perception task by requiring subjects to discriminate between a small number of items rather than many.

We initially tested our patients on a number of simple face and non-face perceptual judgment tasks requiring them to make judgments about facial attractiveness, age, and gender. The stimuli used in these studies were computer generated although highly realistic and varied only on the dimension of interest. On these tasks, the patients performed normally, even when they were required to make comparisons between stimuli with a high degree of feature overlap. Because these are null results, we do not report them here; however, they served as a springboard for the following four experiments.

In three of our experiments, facial stimuli were tested. Facial stimuli were chosen because there is evidence that the ATL has an important role in aspects of face processing (Olson, McCoy, Klobusicky, & Ross, 2013; Olson et al., 2007) and also because Lee, Bussey, et al. (2005) reported that PRC lesions impair face perception when similar faces are used as stimuli. In Experiment 4, we test discrimination of dot patterns in order to assess the generality of the findings from face stimuli. The similarity of all stimuli was parametrically varied in all tasks because it has been claimed that the PRC is involved only in perception tasks that require differentiating items with a high degree of feature overlap, in processing feature conjunctions, or in making difficult or fine visual discriminations (e.g. Buckley & Gaffan, 2006). We term these theories "fine discrimination" theories. Although our study is more generally about perceptual functions of the ATL, we apply theories developed for the PRC, given that the anterior boundary of the human PRC is ambiguous (Kirwan & Stark, 2004).

If the ATL is generally important for visual discrimination, patients should perform worse than controls on most visual perception tasks. If the ATL is particularly important for fine visual discrimination, the patient group should suffer relatively more when the degree of similarity or feature overlap between stimuli is high. Last, if the ATL is only involved in face perception, deficits should not be observed for non-face stimuli.

Experiments 1–4: perceptual comparisons

General methods for all experiments

Participants

Patient KN313. Patient KN313 is a right-handed male (age 53, 12 years of education) with unilateral right ATL damage as a result of a basilar artery aneurysm in 1995 (see Table 1). The entire cap of the ATL is damaged; damage extends into the temporal pole, anterior PRC, and the amygdala, as assessed by MRI (see Figure 1). His main complaint is depression, which is successfully treated with Paxil. Prior to treatment, his score on the Beck Depression Inventory was 24, which is the moderate range. At the time of testing he was cheerful although his personality was somewhat eccentric.

Visual acuity was normal (20/20 right eye, 20/30 left eye) without field cuts and he does not self-report any visual problems. His performance on a line cancellation task was normal. His performance on the Visual Object and Space Perception Battery (VOSP) (Warrington & James, 1991) was normal except for the silhouettes subtest, in which the task is to name silhouettes of animals and objects, and the object decision subtest, in which the task is to choose which of four silhouettes represents a real object. His performance on this test was significantly

Table 1. Performance of patient KN313 and KG581 on neuropsychological tests.

Test	Subtest	KN313	KG581
VOSP	Screening test	100%	100%
	Incomplete letters	85%	100%
	Silhouettes	40%*	37%*
	Object decision	60%*	85%
	Progressive silhouettes/20[†]	7	13
	Dot counting	100%	100%
	Position discrimination	95%	95%
	Number location	90%	70%
	Cube analysis	90%	100%
Reading	Normal words	100%	94%
	Exception words	56%*	38%*
	Nonwords	100%	100%
Famous name-face matching		96%	81%
IQ	WAIS	118	–
WMS	Auditory immediate	108	94
	Visual immediate	100	100
	Auditory delayed	99	108
	Visual delayed	97	106

Notes: VOSP = Visual Object and Space Perception Battery (Warrington & James, 1991). WMS = Weschler Memory Scale. WMS scores are index scores in which the population average is 100. An "*" indicates that performance was below the cutoff.

[†] Lower numbers indicate better performance on the progressive silhouettes task.

impaired. Because the silhouettes do not have internal features, his impairment cannot be accurately described as a configuration processing deficit. His reading of exception words was below normal (9/16) while reading of regular words and nonwords was normal (16/16 and 8/8). These findings are consistent with a subtle semantic memory deficit (Lezak, 1995) or a visual association problem of grapheme-to-phoneme conversion.

Because there are reports that right ATL damage impairs face processing (Damasio et al., 1990), especially in the case of famous faces (Fukatsu, Fujii, Tsukiura, Yamadori, & Otsuki, 1999; Glosser, Salvucci, & Chiaravalloti, 2003; Joubert et al., 2003; Snowden, Thompson, & Neary, 2004; Thompson, Patterson, & Hodges, 2003; Tsukiura et al., 2002), we tested him on a name-face matching task. On each trial, he was given the name of a famous person and had to choose the corresponding face from a group of 10 faces from the same semantic category. For example, one trial required picking Bill Clinton's face out of 10 pictures of politicians. His score on this test (46/48) was high. However, he reports that since his aneurysm "lots of people look alike" to him. He has also previously reported difficulty with directions and landmarks, once getting lost on the way to his mother's house and ending up two doors down. These problems have also diminished over time.

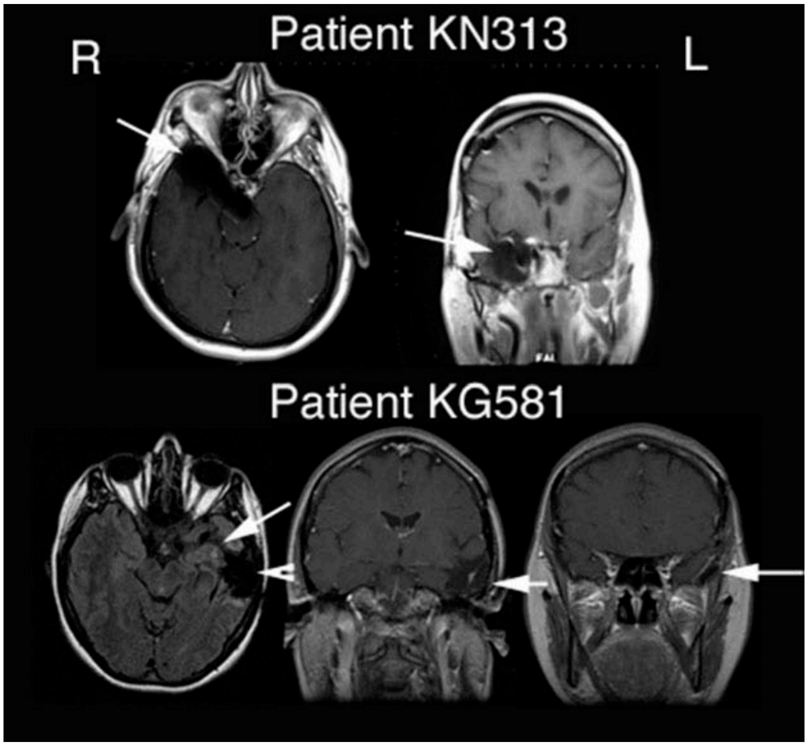

Figure 1. MRI scans from the two patients tested in this study. Scans are shown in radiological convention (e.g. left on the right). Patient KG581's scans are FLAIR images (axial view) or T2-weighted images (coronal view). The resection is clearly evident. More subtle damage from post-surgical changes, including scarring and residual tumor, are also evident.

No episodic or working memory deficits were observed during neuropsychological testing and none were found during administration of the dementia rating scale (DRS)-2. Performance on the Weschler Memory Scale (WMS) was completely normal (see Table 1). His VIQ as tested with the American National Adult Reading Test was 118. Attention, intellectual, or executive impairments were not self-reported or observed, nor were they noted in his neurological reports.

Patient KG581. Patient KG581 is a right-handed female (age 40, 12 years of education) with unilateral left ATL damage as a result of a tumor resection in 2004 (see Table 1). Damage extends into the temporal pole, anterior aspects on the middle temporal gyrus, and the lateral temporal lobe, as assessed by MRI (see Figure 1). She does not complain of any mood disorders and is currently medication free. At the time of testing, she was cheerful and attentive.

Visual acuity is normal (20/20 right eye, 20/20 left eye). Her performance on the VOSP was normal except for impairment on the silhouettes subtest. Her reading of exception words was below normal (6/16) while reading of regular words and nonwords was normal (15/16 and 8/8). In her job as a cashier, she frequently fails to recall or recognize the names of low-frequency items such as brands of clothing detergent. As with patient KN313, these findings are consistent with a subtle semantic memory deficit and/or surface dyslexia (Lezak, 1995).

She does not self-report any perceptual problems. Her performance on the famous face test was 39/48, somewhat lower than patient KN313, but not impaired.

No episodic or working memory deficits were observed during neuropsychological testing and none were found during administration of the DRS-2 (Mattis, 1998) and WMS (see Table 1). Attention, intellectual, or executive impairments were not self-reported or observed, nor were they noted in her neurological reports.

Controls. The performance of patients was compared to that of healthy matched controls: Exp. 1 = 13 controls (*M* age = 46, *M* education = 14 years, 7 males); Exp. 2 = 13 controls (*M* age = 46, *M* education = 14 years, 7 males); Exp. 3 = 15 controls (*M* age = 48, *M* education = 15 years, 3 males); Exp 4 = 10 controls (*M* age = 50, *M* education = 14 years, 5 males). There were no age or education differences between ATL patients and controls (all *p*s > .15). Control participants were cooperative and attentive and had normal or corrected-to-normal visual acuity. All signed an informed consent form prior to taking part in the experiment. Many of them participated in every experiment.

Materials. Experiment 1: Stimuli were 72 bitmap images of black circles ranging in diameter from 1.42 to 3.53 cm (see Figure 2). Stimuli were pilot tested on naïve subjects. Experiment 2: Stimuli were morphed faces that varied along the dimension of age; Experiment 3: Stimuli were morphed faces that varied along the dimension of identity (see Figure 2). Male faces were used. Experiment 4: Stimuli were dot clouds that varied in configural similarity.

Morphed faces were created with GenHead software (www.genemation.com/). This software creates highly realistic artificial faces across 114 parameters, each an eigenvector derived from a principal components analysis of a large database of face photographs. Additional parameters allow control of gender, age, and ethnicity. The stimuli were created as follows: 16 Caucasian faces were generated with a distance of 6.000, male and female. Two dissimilar faces from the 16 were selected to be the base pair for each set (denoted base 1 and base 2) and morphs were created by titrating the percentage of base 2's face that was added to base 1's face. This process was continued until there were 32 morphed sets of male and female faces that varied along the dimension of identity (between sets). Faces were 105 mm × 124 mm in size at a resolution of 72 pixels/inch and 32 bits/pixel. They were presented on a uniformly black background.

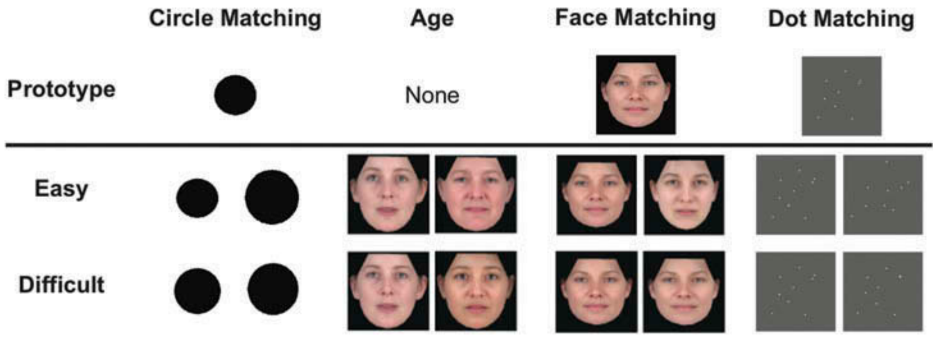

Figure 2. A schematic illustration of the stimuli and task used in: (from left to right) Experiment 1, circle judgment task; Experiment 2, age judgment task; Experiment 3, face identity judgment task; and Experiment 4, dot configuration judgment task. [To view this figure in color, please see the online version of this Journal.]

Dot clouds were created in Matlab (www.mathworks.com) using the Psychophysics Toolbox (www.psychtoolbox.org). Each dot cloud consisted of nine white dots clustered to form an abstract configuration. Each dot was 5 pixels in diameter; the size of the entire dot pattern was approximately 200 × 200 pixels. Dot clouds were created as sets that consisted of a single "canonical" image and 10 "morph" images. The coordinates of the dots in the canonical images were randomly generated. Each morph image was created by perturbing the original canonical dot coordinates; this created a visible pattern of decay from first to last morph and offered flexibility in choosing stimuli for the task. For each dot, one of four directions (up, down, left, and right) was randomly chosen as the direction of "jitter." Each dot was then moved by a fixed number of pixels in the randomly chosen direction. We created varying degrees of morph by incrementally varying the amount of displacement each dot received. All dot patterns were presented on the same uniform gray background.

Equipment. Participants were tested individually on either a laptop computer or a desktop computer, under normal lighting conditions. They sat at an unrestricted viewing distance of about 57 cm, at which distance 1 cm corresponds to 1° viewing angle. All experiments were programmed in E-Prime.

Design. On each trial, one sample stimulus was presented above two side-by-side probe stimuli. The task was to choose the probe stimulus that was most similar to the sample stimulus on the dimension of interest. There was an 8-s time limit per trial. On easy trials, the two stimuli were quite different from one another; on difficult trials, the two probe stimuli were very similar. The dimension of interest was varied continuously but was later binned into four levels of difficulty for analysis. The side of the "match" stimulus was counterbalanced across trials. The dimensions of interest were: Experiment 1: size; Experiment 2: age; Experiment 3: facial identity; and Experiment 4: dot cloud configuration. In each experiment, there were four levels of difficulty, depending on how similar the two probe stimuli were on the dimension of interest (level 4 = most similar). Across the different experiments, the trial numbers were: 80, 64, 187, and 96.

Analysis. In addition to the between-subject variable (patient vs. control), similarity/difficulty (ranging from 1, very different, to 4, very similar) was manipulated. We did not analyze response times (RTs) because both of the patients were unfamiliar with using a mouse, potentially leading to systematic differences in RTs between patients and controls.

Data were analyzed with nonparametric permutation tests because standard nonparametric tests were not available for our task deign. Permutation tests are frequently used in neuroimaging and computational biology. For these data, the F-statistic under the standard mixed two-factor ANOVA model was computed. The observed values were then randomly permuted across the subjects and for the treatment within each subject. The F-statistics were recomputed for the permuted dataset and a one-tailed count over 1000 replicates was used to compute the significance values. A few things to note: because our permutation test was based on an ANOVA model, it is inappropriate to apply this test to a single-subject design. Also, the F-statistics can be quite large and degrees of freedom are not conventionally reported. More information about permutation tests is available at http://en.wikipedia.org/wiki/Resampling_(statistics). It should be noted that in all experiments, similar effects were observed when parametric tests were conducted.

Results

Data for all studies are depicted in Figure 3.

Experiment 1: circle size

Across all study participants, higher levels of stimulus similarity led to lower rates of accuracy, $F = 38.843$, $p < .0001$. However, as a group, patients exhibited similar levels of accuracy as controls, $F = 173.415$, $p = .260$. The interaction of group × similarity was not significant, $F < 1$, *ns*.

Experiment 2: facial age

Subjects were generally impaired by higher levels of similarity, $F = 20.778$, $p < .0001$. Of interest here, the patients exhibited similar levels of accuracy as controls, $F = 1.552$, $p = .673$. The interaction of group × similarity was not significant, $F = 1.968$, $p = .126$.

Experiment 3: facial identity

Overall, subjects were impaired by higher levels of similarity, $F = 25.568$, $p < .0001$. The patients performed at lower accuracy levels than controls (10% less accurate, $F = 858.44$, $p = .039$) but were not differentially sensitive to the similarity manipulation (group × similarity interaction, $F = 1.995$, $p = .133$).

Experiment 4: dot cloud identity

Subjects were generally impaired by higher levels of similarity, $F = 27.056$, $p < .0001$. Of interest here, the ATL patients were on average 9.5% less accurate than controls, $F = 25.334$, $p = .045$. However, once again, the interaction of

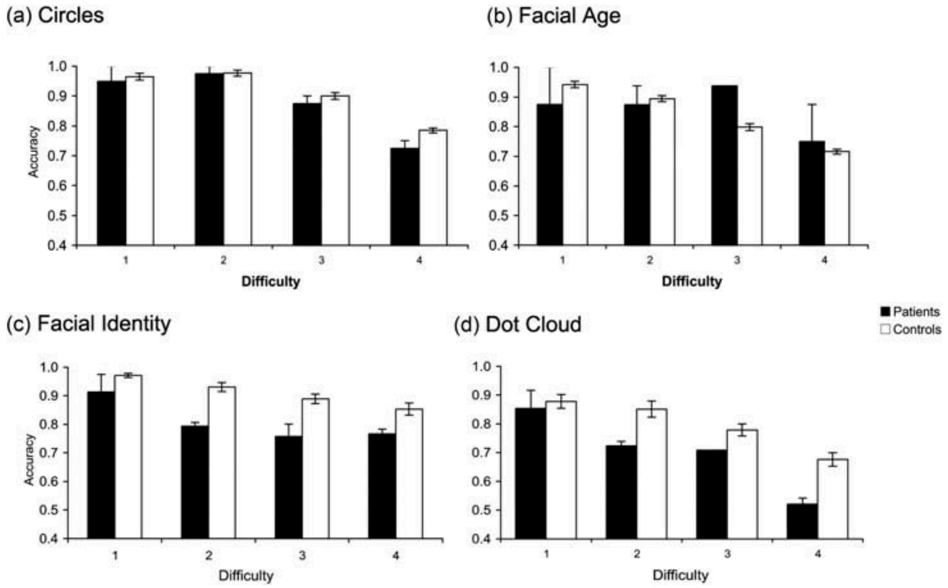

Figure 3. Results of all experiments. Difficulty level is depicted on the *x*-axis, and accuracy is depicted on the *y*-axis. Difficulty was manipulated by making sample images more or less physically similar to a sample image. Task performance on four studies is depicted (a) circle size judgment task, (b) facial age judgment task, (c) facial identity judgment task, (d) dot configuration judgment task. Patients were worse than controls on the facial identity and dot configuration tasks.

group × similarity was not significant, $F = 1.179$, $p = .329$. We note that in a pilot study, we tested participants on a task and stimulus set similar to that used in Experiment 4, except with no time limit. Accuracy was emphasized over speed. The patients showed dramatically longer RTs than controls (mean = 15,170 ms vs. 8,651 ms, $p = .022$), but no accuracy differences. Together these findings suggest that the patients had great difficulty with comparing the dot-cloud stimuli. Depending on task parameters, either a speed or an accuracy deficit was demonstrated.

These results show that difficulties judging facial identity described in Experiment 3 are also found for non-face stimuli that require configural processing.

General discussion

The results of these studies show that unilateral ATL damage can cause perceptual deficits under some conditions (Table 2). In our pilot studies, we found that when making a simple unidirectional judgment, such as deciding whether a face is male or female, patients with ATL damage performed just like controls. Intact performance was observed even on more difficult trials. Likewise, ATL damage does not impair the ability to decide which of two probe stimuli is most like a sample stimulus when stimuli can be differentiated on the basis of simple features such as size (Exp. 1) or simple facial features such as differences in nasal-labial folds that are indicative of facial aging (Exp. 2). Although there are many facial features that change with age, in our GenHead stimulus set, changes in nasal-labial folds were one of the primary features that were manipulated. However, when making the same decision with stimuli that required a comparison across multiple features, such as faces differing in their identity (Exp. 3) or dot clouds (similar to those used by Posner and Keele in their classic study of category formation (Posner & Keele, 1968)), patients with ATL damage were impaired (Exp. 4). Unexpectedly, ATL damage did not disproportionately impair performance on trials in which feature ambiguity/perceptual similarity was high. In the next paragraphs, we describe four "take-home" messages derived from our findings.

Table 2. Summary of experimental findings.

Experimental task	Stimuli	Patients impaired?
Perceptual comparison	1. Circles, varying size	No
	2. Faces, varying age	No
	3. Faces, varying identity	Yes
	4. Dots, varying configuration	Yes

Point 1: ATL damage causes a specific type of face perception deficit: a deficit for apprehending facial identity

Our patients performed normally on many face perception tasks in pilot studies, as well as on a face-age task, but abnormally when required to make difficult identity judgments about faces or dot clouds. Our findings are in line with those of Fox, Hanif, Iaria, Duchaine, and Barton (2011) who tested two patients with ATL damage (patients B-AT1 and R-AT1) and reported normal face matching performance on the Benton Face Inventory and normal facial expression perception, but abnormally low face-identity discrimination on task that used morphed faces.

Point 2: the patients' perceptual deficits cannot be described as face-specific

Since the patients' accuracy was abnormally low on a task that required the comparison of complex non-face stimuli (dot clouds, Exp. 4) their perceptual deficits cannot be described as face-specific. The dot clouds were created because similarity could only be judged by analyzing all features, not one. We noticed in an untimed pilot study using the same dot cloud stimuli that the patients had dramatically longer RTs than controls (mean = 15,170 ms vs. 8,651 ms, $p = .022$) because they tended to use a time-consuming dot-by-dot comparison strategy to perform the task. Although we don't wish to put too much stock in the patient's RTs, given their unfamiliarity with using a computer mouse, this finding hints that their ability to perceive and process visual stimuli can be characterized as overly focused on details with difficulties integrating over multiple features.

Point 3: facial identity deficits after ATL damage may be caused by a fundamental problem in visual configural processing; face identity may be the canonical stimulus type that relies on this type of processing

Some judgments about faces, such as age discrimination, can be performed by quickly comparing one or two diagnostic features (for review, see Rhodes, 2013). In contrast, judgments of facial identity similarity require one to compare all the details of an entire object. Neurons in the vATL of the monkey have unusual receptive field properties that speak to this issue: when a monkey fixates an object in a cluttered scene, the normally large receptive field rapidly shrinks (Rolls, Aggelopoulos, & Zheng, 2003). This property may allow for both object selection when the receptive field is large, and fine discrimination of the selected object when the receptive field is small. Thus, vATL damage may impair the ability to make fine grained discriminations based on a gestalt/configuration because unconnected parts can no longer be accurately combined.

Point 4: there is converging evidence that a region in vATL has a critical role in high level face processing

Recent fMRI studies reported the existence of two face-sensitive patches in the macaque vATL and human vATL (reviewed by Von der Heide et al., 2013). However, the perceptual properties of this region appear to be constrained because cells in the monkey vATL are only sensitive to certain perceptual manipulations such as changes in facial identity, but not to perceptual changes that leave identity intact (Eifuku, De Souza, Nakata, Ono, & Tamura, 2011; Eifuku, Nakata, Sugimori, Ono, & Tamura, 2010). Thus, although the vATL does appear to be part of a larger network for perceptual face discrimination, its sensitivity is distinct from that of more posterior regions such as the fusiform gyrus, which are sensitive to lower level perceptual changes.

Recent findings indicate that the vATL face patch is within the confines of classically defined PRC (Collins & Olson, 2014; O'Neil, Hutchison, McLean, & Kohler, 2014). Interestingly, PRC deterioration is found in the earliest stages of Alzheimer's disease as well as semantic dementia. Whether these disorders are also accompanied by visual perceptual problems early in the disease course has not been widely discussed.

Laterality effects

Humans with ATL damage often have face memory deficits (Damasio et al., 1990). Left-lateralized lesions tended to affect lexical aspects of person memory, such as recollection of names, while right-lateralized lesions tended to affect feelings of familiarity and processing and retrieval of biographical information. It has recently been argued that the right ATL participates more in pictorial representations of people (Gainotti, 2012). The two ATLs are connected via the anterior commissure so it is likely that there is a great deal of information exchange between the two hemispheres with a relative bias toward processing pictorial aspects of people in the right ATL, and a relative bias toward processing verbal aspects of people in the left ATL. Although our patients performed similarly on most tasks, our patient with left ATL lesions reported some word-finding problems while our patient with right ATL lesions reported that sometimes people all looked the same.

Shortcomings of the present study

One shortcoming of the present study is that the number of trials per participant was small, and there were different numbers of trials across tasks. There were fewer trials in Exp. 1 and 2, in which null results were obtained, as compared to Exp. 3 and 4, where positive results were obtained. The variability in Exp. 1 was low, with all participants performing at a uniformly high level so we do not believe that the number of trials was too low. However, in Exp. 2, the facial age study, there was more variability among the patients at the easiest and hardest difficulty levels, suggesting that the patients may have adopted a quixotic strategy to perform this task. Future investigators may wish to look into this further.

Conclusions

In sum, our findings indicate that the ATL has a role in high-level visual perception. Its role is evident only on tasks requiring the comparison of similar entities distinguishable by gestalt-level differences. These findings also suggest that the vATL may play an important, albeit largely unrecognized, role in face perception.

Acknowledgments

We would like to thank David Drowos and Govinda Vyas for assistance with testing and figure creation. We would also like to thank our patient group who generously donated their time.

Disclosure statement

The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institute of Mental Health or the National Institutes of Health.

Funding

This work was supported by a National Institute of Health grant to I. Olson [grant number RO1 MH091113].

References

Barense, M. D., Bussey, T. J., Lee, A. C. H., Rogers, T. T., Davies, R. R., Saksida, L. M., … Graham, K. S. (2005). Functional specialization in the human medial temporal lobe. *The Journal of Neuroscience*, *25*, 10239–10246. doi:10.1523/JNEUROSCI.2704-05.2005

Buckley, M. J., Booth, M. C. A., Rolls, E. T., & Gaffan, D. (2001). Selective perceptual impairments after perirhinal cortex ablation. *Journal of Neuroscience*, *21*, 9824–9836.

Buckley, M. J., & Gaffan, D. (2006). Perirhinal cortical contributions to object perception. *Trends in Cognitive Sciences*, *10*, 100–107. doi:10.1016/j.tics.2006.01.008

Buffalo, E. A., Reber, P. J., & Squire, L. R. (1998). The human perirhinal cortex and recognition memory. *Hippocampus*, *8*, 330–339. doi:10.1002/(SICI)1098-1063(1998)8:4<330::AID-HIPO3>3.0.CO;2-L

Bussey, T. J., & Saksida, L. M. (2002). The organization of visual object representations: A connectionist model of effects of lesions in perirhinal cortex. *European Journal of Neuroscience*, *15*, 355–364. doi:10.1046/j.0953-816x.2001.01850.x

Bussey, T. J., Saksida, L. M., & Murray, E. A. (2006). The perceptual-mnemonic/feature conjunction model of perirhinal cortex function. *Quarterly Journal of Experimental Psychology*, *58B*, 269–282.

Collins, J., & Olson, I. R. (2014, April). *Beyond the FFA: The role of the ventral anterior temporal lobe in face processing*. Cognitive Neuroscience Society, Boston, MA.

Damasio, A. R., Tranel, D., & Damasio, H. (1990). Face agnosia and the neural substrates of memory. *Annual Review of Neuroscience*, *13*, 89–109. doi:10.1146/annurev.ne.13.030190.000513

Eifuku, S., De Souza, W. C., Nakata, R., Ono, T., & Tamura, R. (2011). Neural representations of personally familiar and unfamiliar faces in the anterior inferior temporal cortex of monkeys. *PLoS ONE*, *6*, e18913. doi:10.1371/journal.pone.0018913

Eifuku, S., Nakata, R., Sugimori, M., Ono, T., & Tamura, R. (2010). Neural correlates of associative face memory in the anterior inferior temporal cortex of monkeys. *Journal of Neuroscience*, *30*, 15085–15096. doi:10.1523/JNEUROSCI.0471-10.2010

Fox, C. J., Hanif, H. M., Iaria, G., Duchaine, B. C., & Barton, J. J. (2011). Perceptual and anatomic patterns of selective deficits in facial identity and expression processing. *Neuropsychologia*, *49*, 3188–3200. doi:10.1016/j.neuropsychologia.2011.07.018

Fukatsu, R., Fujii, T., Tsukiura, T., Yamadori, A., & Otsuki, T. (1999). Proper name anomia after left temporal lobectomy: A patient study. *Neurology*, *52*, 1096–1099. doi:10.1212/WNL.52.5.1096

Gainotti, G. (2012). The format of conceptual representations disrupted in semantic dementia: A position paper. *Cortex*, *48*, 521–529. doi:10.1016/j.cortex.2011.06.019

Glosser, G., Salvucci, A. E., & Chiaravalloti, N. D. (2003). Naming and recognizing famous faces in temporal lobe epilepsy. *Neurology*, *61*, 81–86. doi:10.1212/01.WNL.0000073621.18013.E1

Graham, K. S., Simons, J. S., Pratt, K. H., Patterson, K., & Hodges, J. R. (2000). Insights from semantic dementia on the relationship between episodic and semantic memory. *Neuropsychologia*, *38*, 313–324. doi:10.1016/S0028-3932(99)00073-1

Hampton, R. R. (2005). Monkey perirhinal cortex is critical for visual memory, but not for visual perception: Reexamination of the behavioural evidence from monkeys. *The Quarterly Journal of Experimental Psychology: Section B*, *58*, 283–299. doi:10.1080/02724990444000195

Holdstock, J. S., Gutnikov, S. A., Gaffan, D., & Mayes, A. R. (2000). Perceptual and mnemonic matching-to-sample in humans: Contributions of the hippocampus, perirhinal and other medial temporal lobe cortices. *Cortex*, *36*, 301–322. doi:10.1016/S0010-9452(08)70843-8

Joubert, S., Felician, O., Barbeau, E., Sontheimer, A., Barton, J. J., … Poncet, M. (2003). Impaired configurational processing in a case of progressive prosopagnosia associated with predominant right temporal lobe atrophy. *Brain*, *126*, 2537–2550. doi:10.1093/brain/awg259

Kimura, D. (1963). Right temporal-lobe damage. Perception of unfamiliar stimuli after damage. *Archives of Neurology*, *8*, 264–271. doi:10.1001/archneur.1963.00460030048004

Kirwan, C. B., & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. *Hippocampus*, *14*, 919–930. doi:10.1002/hipo.20014

Kondo, H., Saleem, K. S., & Price, J. L. (2003). Differential connections of the temporal pole with the orbital and medial prefrontal networks in macaque monkeys. *The Journal of Comparative Neurology*, *465*, 499–523. doi:10.1002/cne.10842

Kondo, H., Saleem, K. S., & Price, J. L. (2005). Differential connections of the perirhinal and parahippocampal cortex with the orbital and medial prefrontal networks in macaque monkeys. *The Journal of Comparative Neurology*, *493*, 479–509. doi:10.1002/cne.20796

Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: An expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences*, *17*, 26–49. doi:10.1016/j.tics.2012.10.011

Lansdell, H. (1968). Effect of extent of temporal lobe ablations on two lateralized deficits. *Physiology & Behavior*, *3*, 271–273. doi:10.1016/0031-9384(68)90097-8

Lee, A. C. H., Barense, M. D., & Graham, K. S. (2005). The contribution of the human medial temporal lobe to perception: Bridging the gap between animal and human studies. *The Quarterly Journal of Experimental Psychology: Section B*, *58*, 300–325. doi:10.1080/02724990444000168

Lee, A. C. H., Buckley, M. J., Gaffan, D., Emery, T., Hodges, J. R., & Graham, K. S. (2006). Differentiating the roles of the hippocampus and perirhinal cortex in processes beyond long-term declarative memory: A double dissociation in dementia. *The Journal of Neuroscience*, *26*, 5198–5203. doi:10.1523/JNEUROSCI.3157-05.2006

Lee, A. C. H., Buckley, M. J., Pegman, S. J., Spiers, H., Scahill, V. L., Gaffan, D., … Graham, K. S. (2005). Specialization in the medial temporal lobe for processing of objects and scenes. *Hippocampus*, *15*, 782–797. doi:10.1002/hipo.20101

Lee, A. C. H., Bussey, T. J., Murray, E. A., Saksida, L. M., Epstein, R. A., Kapur, N., … Graham, K. S. (2005). Perceptual deficits in amnesia: Challenging the medial temporal lobe "mnemonic" view. *Neuropsychologia*, *43*, 1–11. doi:10.1016/j.neuropsychologia.2004.07.017

Levy, D. A., Shrager, Y., & Squire, L. R. (2005). Intact visual discrimination of complex and feature-ambiguous stimuli in the absence of perirhinal cortex. *Learning and Memory*, *12*, 61–66. doi:10.1101/lm.84405

Lezak, M. (1995). *Neuropsychological assessment* (3rd ed.). New York, NY: Oxford University Press.

Mattis, S. (1998). *Dementia rating scale*. Odessa, FL: Psychological Assessment Resources.

Meier, M. J., & French, L. (1965). Lateralized deficits in complex visual discrimination and bilateral transfer of reminiscence following unilateral temporal lobectomy. *Neuropsychologia*, *3*, 261–272. doi:10.1016/0028-3932(65)90028-X

Murray, E. A., & Bussey, T. J. (1999). Perceptual-mnemonic functions of the perirhinal cortex. *Trends in Cognitive Sciences*, *3*, 142–151. doi:10.1016/S1364-6613(99)01303-0

Nakamura, K., & Kubota, K. (1996). The primate temporal pole: Its putative role in object recognition and memory. *Behavioural Brain Research*, *77*, 53–77. doi:10.1016/0166-4328(95)00227-8

O'Neil, E. B., Hutchison, R. M., McLean, D. A., & Kohler, S. (2014). Resting-state fMRI reveals functional connectivity between face-selective perirhinal cortex and the fusiform face area related to face inversion. *Neuroimage*, [Epub]. doi:10.1016/j.neuroimage.2014.02.005

Olson, I. R., McCoy, D., Klobusicky, E., & Ross, L. A. (2013). Social cognition and the anterior temporal lobes: A review and theoretical framework. *Social Cognitive Affective Neuroscience*, *8*, 123–133. doi:10.1093/scan/nss119

Olson, I. R., Plotzker, A., & Ezzyat, Y. (2007). The enigmatic temporal pole: A review of findings on social and emotional processing. *Brain*, *130*, 1718–1731. doi:10.1093/brain/awm052

Patterson, K. (2007). The reign of typicality in semantic memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*, 813–821.

Posner, M. I., & Keele, S. W. (1968). On the genesis of abstract ideas. *Journal of Experimental Psychology*, *77*, 353–363. doi:10.1037/h0025953

Rhodes, G. (2013). Looking at faces: First-order and second-order features as determinants of facial appearance. *Perception*, *42*, 1179–1199.

Rolls, E. T., Aggelopoulos, N. C., & Zheng, F. (2003). The receptive fields of inferior temporal cortex neurons in natural scenes. *Journal of Neuroscience*, *23*, 339–348.

Snowden, J. S., Thompson, J. C., & Neary, D. (2004). Knowledge of famous faces and names in semantic dementia. *Brain*, *127*, 860–872. doi:10.1093/brain/awh099

Squire, L. R., & Zola-Morgan, S. (1991). The medial temporal lobe memory system. *Science*, *253*, 1380–1386. doi:10.1126/science.1896849

Stark, C. E., & Squire, L. R. (2000). Intact visual perceptual discrimination in humans in the absence of perirhinal cortex. *Learning and Memory*, *7*, 273–278. doi:10.1101/lm.35000

Thompson, S. A., Patterson, K., & Hodges, J. R. (2003). Left/right asymmetry of atrophy in semantic dementia: Behavioral-cognitive implications. *Neurology*, *61*, 1196–1203. doi:10.1212/01.WNL.0000091868.28557.B8

Tsukiura, T., Fujii, T., Fukatsu, R., Otsuki, T., Okuda, J., Umetsu, A., … Yamadori, A. (2002). Neural basis of the retrieval of people's names: Evidence from brain-damaged patients and fMRI. *Journal of Cognitive Neuroscience*, *14*, 922–937.

Von der Heide, R. J., Skipper, L. M., & Olson, I. R. (2013). Anterior temporal face patches: A meta-analysis and empirical study. *Frontiers in Human Neuroscience*, *7*, 17. doi:10.3389/fnhum.2013.00017

Warrington, E. K., & James, M. (1991). *The visual object and space perception battery: Manual*. Suffolk: Thames Valley Test Company.