Bilateral hemispheric representation of words and faces: Evidence from word impairments in prosopagnosia and face impairments in pure alexia

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Abstract

Considerable research has supported the view that faces and words are subserved by independent neural mechanisms located in the ventral visual cortex in opposite hemispheres. On this view, right hemisphere ventral lesions that impair face recognition (prosopagnosia) should leave word recognition unaffected, and left hemisphere ventral lesions that impair word recognition (pure alexia) should leave face recognition unaffected. The current study shows that neither of these predictions were upheld. A series of experiments characterizing speed and accuracy of word and face recognition were conducted in seven patients (four pure alexic, three prosopagnosic) and matched controls. Prosopagnosic patients revealed mild but reliable word recognition deficits, and pure alexic patients demonstrated mild but reliable face recognition deficits. The apparent co-mingling of face and word mechanisms is unexpected from a domain-specific perspective, but follows naturally as a consequence of an interactive, learning-based account in which neural representations for both faces and words are the result of an optimization procedure embodying specific computational principles and constraints.

Introduction

Two opposing theoretical perspectives have been offered to explain the manner by which biological structures, such as the human ventral visual cortex, come to be functionally optimized in the service of visual object recognition. The first perspective argues that there are distinct cortical modules or regions, which mediate behavioral processes, such as face, or word, or object recognition, in a domain-specific manner (Kanwisher, 2010; McKone & Robbins, 2011). Consistent with this approach are the findings that different areas in ventral visual cortex respond selectively to particular categories of visual stimuli: for example, as evident from many fMRI studies, the fusiform face area (FFA) is selectively activated in response to faces (Kanwisher, McDermott, & Chun, 1997; Puce, Allison, Gore, & McCarthy, 1995), the parahippocampal place area (PPA) to scenes (Epstein, 2011; Epstein, Harris, Stanley, & Kanwisher, 1999; Sewards, 2011), and the extrastriate body area (EBA) and fusiform body area (FBA) to human bodies and body parts (Peelen & Downing, 2005; Schwarzlose, Baker, & Kanwisher, 2005; Willems, Peelen, & Hagoort, 2010). Indeed, in each of these regions, the BOLD response for the preferred category is about twice that for the non-preferred category. Moreover, these domain-selective responses are evident in most individuals and these patterns of selectivity are observed across many different studies conducted by many different investigators using a host of different paradigms.

The second perspective acknowledges the apparent selectivity of neural areas for certain visual classes, but argues that this selectivity need not implicate specialized modules per se. On this account, there exists a many-to-many arrangement, in which multiple regions mediate the recognition of a particular object type (e.g., faces) and in which any single region represents multiple object types, albeit to varying degrees (Ishai, Ungerleider, & Haxby, 2000). Consistent with this perspective, fMRI studies have demonstrated that, in addition to the FFA, multiple cortical regions evince face-selectivity, including the occipital face area (OFA) (Gauthier et al., 2000), the posterior superior temporal sulcus (Haxby, Hoffman, & Gobbini, 2000) and the anterior temporal lobe (Kriegeskorte, Formisano, Sorger, & Goebel, 2007; Rajimehr, Young, & Tootell, 2009) [see also (Atkinson & Adolphs, 2011; Avidan & Behrmann, 2009; Haxby & Gobbini, 2007)]. Additionally, even

highly selective regions, such as the FFA, evince a BOLD response to different object classes, albeit with lesser activation (Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999; Grill-Spector, Sayres, & Ress, 2006; Hanson & Schmidt, 2011; Haxby et al., 2011; Ishai, Ungerleider, Martin, & Haxby, 2000; Nestor, Plaut, & Behrmann, 2011). Thus, even within a region, specialization is more graded than binary and a particular region may be optimized for, but not necessarily devoted to, a distinct cognitive function (Haxby, Grady, Ungerleider, & Horwitz, 1991).

Here, we examine the extent of the specificity of the neural substrate subserving the recognition of two classes of objects, words and faces. We chose these two classes because, intuitively, they appear to be diametrically opposed, obviously differing in overt geometry and image statistics. Additionally, faces and words diverge substantially in their acquisition, as face recognition develops incidentally whereas, for most individuals, word recognition is acquired through specific instruction in a more formal schooling environment. Finally, the evolutionary status of words and faces varies: whereas reading is a relatively recent invention, introduced approximately 5400 years ago (Dehaene & Cohen, 2007), this is not the case for face recognition.

Domain specificity: Words and faces

From a domain-specific perspective, words and faces are each assumed to be subserved by a particular, distinct cortical region. The Visual Word Form Area (VWFA), considered the pre-eminent region underlying word recognition is located roughly at Talairach coordinates x=-43, y=-54, z=-12 in the left hemisphere, and is identifiable even in single subjects (Puce, Allison, Asgari, Gore, & McCarthy, 1996). The VWFA is activated by visual but not auditory words (Cohen & Dehaene, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005; although see Price & Devline, 2011), to a greater degree for letters than digits (Polk et al., 2002) or visually equivalent pseudo-letters (Allison, McCarthy, Nobre, Puce, & Belger, 1994; Cohen & Dehaene, 2004). VWFA activation is rapid, occurring around 150-200 ms post-onset, as shown by ERP (McCandliss, Cohen, & Dehaene, 2003) and MEG (Marinkovic et al., 2003), and its response is relatively insensitive to retinal position and stimulus font, size or case (Polk & Farah, 2002).

Homologously, the Fusiform Face Area (FFA), with peak activation at roughly Talairach coordinates x= 40, y=-55, z=-10 in the right hemisphere, responds more strongly to upright than inverted faces or other non-face objects (Kanwisher, et al., 1997; Kanwisher, Stanley, & Harris, 1999; Schwarzlose, et al., 2005; Sergent, Ohta, & MacDonald, 1992; Sergent & Signoret, 1992a). FFA activation is highly stable within-individual and is correlated with face recognition ability (Yovel, Tambini, & Brandman, 2008).

Additional support for a regionally selective signature for words and for faces comes from neuropsychological investigations in which patients with unilateral lesions to the structural equivalents of the VWFA, on the left, or the FFA, on the right, evince specific behavioral impairments (Kleinschmidt & Cohen, 2006). Thus, patients with a lesion to the left occipital temporal area, specifically along the fusiform and adjacent lingual gyri with possible incursion to the inferior longitudinal fasciculus (Barton, 2011; Cohen et al., 2004; Cohen et al., 2003; Feinberg, Schindler, Ochoa, Kwan, & Farah, 1994; Salvan et al., 2004), have 'pure alexia'. These patients read in a halting, laborious fashion, using a letter-by-letter strategy, and there is a strong linear relationship between their speed (or accuracy) and the length of the word or letter string (for example, see Montant & Behrmann, 2001).

Correspondingly, a lesion to the inferior right temporal lobe results in prosopagnosia (Barton, 2011; Bodamer, 1947; Marotta, Behrmann, & Genovese, 2001; Sergent & Signoret, 1992b), an impairment in face recognition despite intact sensory vision and with normal semantic and naming performance. Salient cues such as facial hair, clothing or hairstyle are used to identify individuals, and gait and voice serve as useful complementary cues. Most cases of prosopagnosia have damage in the vicinity of the lingual and fusiform gyri (Damasio, Damasio, & Hoesen, 1982; Meadows, 1974), a conclusion supported by a meta-analysis (Bouvier & Engel, 2006) and survey of cases (Barton, 2008), and, although some cases have bilateral lesions, the growing consensus is that a right hemisphere lesion alone is sufficient to give rise to prosopagnosia.

Distributed circuits: Words and faces

In contrast with the claim that the cortical structures responsible for human visual recognition contain domain-specific regions, others have argued for more distributed systems with subregions optimized for, but not dedicated to, representing particular stimulus classes. For example, there is a growing body of work showing that words activate a large swath of ventral cortex, beyond just the VWFA itself (Nazir, Ben-Boutayab, Decoppet, Deutsch, & Frost, 2004; Nestor, et al., 2011), with one hypothesis suggesting that this posterior-to-anterior axis serves to represent letters in increasing larger combinations (Dehaene & Cohen, 2011; Vinckier et al., 2007). Exposure to letter-like inputs even affects the tuning properties of V1 neurons (Sigman et al., 2005). Consistent with the graded organization of even a single region, the VWFA is activated not just by orthographic input but also by other stimuli, for example, line drawings (Kherif, Josse, & Price; Price & Devlin, 2003; Wright et al., 2008) and pictures (Braet, Wagemans, & Op de Beeck, 2012), and even faces (Nestor, Behrmann, & Plaut, submitted manuscript). Predictably then, patients with VWFA lesions are impaired in their perception of digits (Starrfelt & Behrmann, 2011) and objects (for example, Behrmann, Nelson, & Sekuler, 1998; Starrfelt & Gerlach, 2007; Starrfelt et al., 2009), as well.

Similarly, recent studies have provided evidence that face recognition is mediated by a distributed neural network consisting of a number of areas including the FFA, a lateral occipital region (OFA), and the superior temporal sulcus (STS), as well as anterior extended regions, including the anterior temporal lobe (Avidan & Behrmann, 2009; Kriegeskorte, Formisano, Sorge, & Goebel, 2007; Nestor, et al., 2011; Nestor, Plaut, & Behrmann, in press; Rajimehr, et al., 2009; Thomas et al., 2009). Moreover, a focal lesion to regions other than the FFA, such as to the anterior temporal lobe (Barton, 2008; Bukach, Bub, Gauthier, & Tarr, 2006; Williams, Savage, & Halmagyi, 2006) can result in prosopagnosia as can a structural disconnection between the FFA and this anterior region (Thomas et al., 2008). Patients with prosopagnosia may also show impaired recognition of other stimulus class, such as Greebles or common objects (Behrmann, Marotta, Gauthier, Tarr, & McKeeff, 2005).

Lateralization

Although there seems to be increasing agreement that the recognition of words and of faces are each mediated by a more distributed than modular system, the current view is still that these two stimulus classes are largely subserved by separate, and largely independent circuits, with words lateralized to the left and faces lateralized to the right hemisphere.

Close scrutiny of some imaging studies, however, suggests that these two apparently disparate classes of visual stimuli might be less lateralized than assumed to date. For example, many fMRI and ERP studies show bilateral activation for words and for faces, albeit usually with greater activation for words on the left and faces on the right side (Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Kanwisher, et al., 1997; Kronbichler et al., 2004; Nestor, et al., 2011; Price & Mechelli, 2005; Puce, et al., 1996; Sergent, Ohta, & MacDonald, 1992b; Tagamets, Novick, Chalmers, & Friedman, 2000). Consistent with this, prosopagnosia is more severe following bilateral than unilateral right lesions (Barton, 2008), implicating the left hemisphere in face recognition and prosopagnosia has been reported in a right-hander subsequent to a left hemisphere lesion (Anaki, Kaufman, Freedman, & Moscovitch, 2007; Mattson, Levin, & Grafman, 2000) [for recent review of lesions in prosopagnosia and a theoretical proposal, see (Gainotti & Marra, 2011)]. Finally, the right hemisphere also appears to play a functional role in word recognition as pure alexia has been reported in a right-hander after a unilateral right occipitotemporal lesion (Davous & Boller, 1994; Ogden, 1984). One final example is of a patient with pure alexia whose recovered reading was disrupted by transcranial magnetic stimulation to the right but not to the left hemisphere (Coslett & Monsul, 1994).

In light of the possible engagement not only of the preferred hemisphere (left-words, right-faces) for recognition of words and faces but also, albeit to a lesser degree, of the non-preferred hemisphere (left-faces, right–words), we examined both the word and face recognition skills of individuals with either pure alexia, following a discrete left hemisphere lesion to the vicinity of the VWFA, or prosopagnosia, following a lesion to the right hemisphere vicinity of the FFA. We predicted that, if the cortical systems mediating face and word

recognition are not independent and are distributed across both hemispheres, then we might expect to see co-mingling of the deficits: thus, pure alexic patients should have some measure of face recognition impairment along with their alexia and prosopagnosic patients should have some measure of word recognition impairment along with their face recognition difficulty. Given the well-established hemispheric superiority for words in the left and faces in the right hemispheres, however, the impairment in the 'preferred domain' (words in left and faces in right) should be greater than in the non-preferred domain: thus, the pure alexics should be more impaired at word than face recognition, and the prosopagnosics should show the converse, and both patient groups should be impaired, even in the non-preferred stimulus domain, relative to controls.

Methods

Participants

Two groups of patients participated in this study, one comprised of four individuals with pure alexia and the second comprised of three individuals with prosopagnosia. All seven patients performed within normal limits on the spatial subtests (dot counting, position discrimination, number location, cube analysis) of the Visual Object and Space Perception battery (VOSP; Warrington & James, 1991). All seven also performed within age-matched norm limits on finger-tapping speed (score computed for each hand separately as mean of five trials of 10 secs per trial; see Strauss, Sherman & Spreen, 2006). Matched control participants were also recruited. All participants had normal or corrected-to-normal vision, were right-handed and gave informed consent. The protocol was approved by the IRB of Carnegie Mellon University.

Pure alexia group (Alexia): All four patients (three male) were premorbidly normal readers and none reported obvious problems in face recognition. A single axial slice from a structural MRI scan for each patient is shown in Figure 1 (top row) and, consistent with existing accounts of the disorder, all sustained damage unilaterally to the left inferior temporo-occipital lobe. Importantly, the right hemisphere is structurally intact in all cases. All patients were able to identify letters, as determined by their high accuracy in identifying a single letter, drawn

randomly from the alphabet, presented in the center of a computer screen for 50 ms duration. Three of the four patients exhibited a field defect of some type (see below). Details for each case are provided next.

INSERT FIGURE 1 APPROXIMATELY HERE

DK, a 75-year-old male, suffered a left posterior cerebral artery infarction in 1995 (see Figure 1, top row). He completed 10th grade and worked in a grocery shop post-stroke. DK suffered from a right homonymous hemianopia at the time of this testing and was diagnosed as a letter-by-letter reader in previous research investigations (Behrmann, Nelson, et al., 1998; Behrmann, Plaut, & Nelson, 1998).

EL is a 56-year-old female with a history of mitral valve prolapse. In April 1996, she was admitted to hospital after suffering two embolic events that caused blurred vision, left arm weakness, and slurred speech. EL was diagnosed as having bacterial endocarditis. A 2009 MRI scan reveals a left posterior cerebral artery infarct (see Figure 1, top row). EL suffers from a right upper quadrantanopsia with macular sparing. EL was a reading teacher for dyslexic children. EL was diagnosed previously as a letter-by-letter reader (Behrmann, Nelson, et al., 1998; McKeeff & Behrmann, 2004; Montant & Behrmann, 2001).

FF, an 84 year-old financial analyst suffered a left posterior hemorrhage in 2003, affecting primarily temporal cortex with slight incursion into the parietal lobe (see Figure 1, top row). Following this, he was diagnosed with pure alexia, with some anomia but no frank aphasia. Past medical history was unremarkable and he received rehabilitation for the reading disorder.

SH is a 64-year-old attorney with a past medical history of proximal atrial fibrillation and hypertension. In July 2004, he experienced a sudden onset of right-sided vision loss, dizziness, and headache, and was hospitalized with a right homonymous hemianopsia. An MRI revealed a left thalamus and left occipito-temporal lesion compatible with a left PCA infarct (see Figure 1, top row).

Prosopagnosia group (Prosop): The three patients (all male) were premorbidly normal readers, by self-report, and none complained of a reading impairment. A single axial slice from a MRI scan is shown for each patient in

the bottom row in Figure 1, and, as evident, all three suffered damage to the right inferior temporo-occipital lobe. The lesion site is compatible both with previous studies of prosopagnosia (Barton, 2008) and with the existing findings of face-selectivity regions as revealed by fMRI (see above). All patients had a structurally intact left hemisphere and full visual fields, and all were unimpaired at single letter identification, evaluated in the same way as for the pure alexic patients described above.

SM sustained a closed head injury in a motor vehicle accident at the age of 18. A MRI scan from 2009 indicated a circumscribed lesion in right occipito-posterior temporal cortex in the vicinity of area LOC (see Figure 1, bottom row; for detailed lesion demarcation, see (Konen, Behrmann, Nishimura, & Kastner, 2011)). SM's prosopagnosia is indicated by his impaired performance in the Benton Facial Recognition Test (32/54; normal 41-54). He is unable to recognize pictures of any famous people, despite being able to provide a good verbal identification when presented with their names auditorily. Further details of his medical and neuropsychological history are available in other publications (Behrmann & Kimchi, 2003; Gauthier, Behrmann, & Tarr, 1999; Konen, et al., 2011; Marotta, Genovese, & Behrmann, 2001; Nishimura, Doyle, Humphreys, & Behrmann, 2010).

RN is a 52-year-old right-handed male who suffered a stroke following a myocardial infarction in May 1998. His most recent MR scan (Fig. 1, bottom row) revealed several gross abnormalities (enlarged ventricles, widespread atrophy) and dense inhomogeneities in the right occipitotemporal area. RN performed at the borderline level on the Benton Face Recognition test (score 40/54) and recognized only 4 out of a set of 50 difficult famous faces (his wife, who served as a control, recognized 14 faces) (Humphreys, Avidan, & Behrmann, 2007). Further biographical and performance details are available from other studies in which RN has participated (Behrmann & Kimchi, 2003; Marotta, McKeeff, & Behrmann, 2002).

CR is a 31-year-old right-handed male who suffered from a right temporal lobe abscess with a complicated medical course including a history of Group A toxic shock syndrome, pneumonia, cardiac arrest, candida bacteremia, and metabolic encephalopathy in May 1996. MR scans reveal a lesion consistent with

acute micro-abscesses of the right temporal lobe and medial occipital lobe (see Figure 1, bottom row). CR has other punctate lesions in the right hemisphere (petechial hemorrhage observable along the grey/white junction) but these are not in the ventral cortex. CR has full visual fields but his performance is in the "severely impaired" range on the Benton Facial Recognition tests (scores of 36/54), and he is unable to recognize pictures of any famous people (for example, Bill Clinton). CR has participated in previous studies (Behrmann & Williams, 2007; Gauthier, Behrmann, et al., 1999; Humphreys, et al., 2007; Marotta, Genovese, et al., 2001).

Some of the data reported here on the face processing abilities of a subset of these prosopagnosic individuals have been previously reported (Marotta, et al., 2002).

Control participants:

Control participants, recruited from the volunteer pool at the Osher Life Long Learning Institute at Carnegie Mellon University, or from the academic and neighboring community, were matched to the Alexia and Prosop participants. Two controls matched each patient on age, gender and educational background. The participants were native English speakers with no history of neurological disease or reading or face recognition difficulties. The controls for the Alexia patients were six males and two females, aged 51-75 with a mean age of 64.6. The controls for the Prosop patients were six male individuals, aged 27-54, with a mean age of 37.2 years.

Apparatus and procedure

A Dell laptop with a 15" display, running E-prime, was used for all experiments. Verbal response times were taken via a desktop microphone and the PST Serial Response Box, and manual responses were taken from the keyboard. Accuracy and reaction time (RT) were recorded for all studies. Participants were seated approximately 50cm from the screen for all experiments.

The data from the two patient groups are first compared against their respective controls to establish whether any impairment is present, and then against each other, to assess the severity of any observed impairment. We summarize the results of all the pairwise group comparisons in Table 1. We also

compare each patients against his/her own controls using the modified t-test for examining a single patient data point (Crawford & Garthwaite, 2004), and the outcomes of these single case comparisons are shown in Table 2. Because of the large number of potential t-test comparisons for each single case (each cell in each experiment), we select only the most informative comparison or summary statistic for the comparisons.

Experiment 1: Word reading

Two experiments, one requiring overt naming and the other requiring lexical decision, were conducted.

Experiment 1a: Naming latency

Methods.

Stimuli. A single word appeared centered over fixation for unlimited duration and the participants were required to read it aloud as fast and as accurately or possible. Note that for the Alexia patients with field defects and no macular sparing (DK and SH), and their matched controls, the stimuli were presented to the left visual field with the final letter of the word placed immediately adjacent to fixation. All words were presented in upper-case Geneva 24-point bold font in black on a white background. To assess the effect of word length on RT, sixty words, twenty each of three, five and seven letters, were included. Words subtended visual angles of approximately 0.5^{o} vertically and approximately 1.5^{o}, 2.4^{o}, and 3.6^{o} horizontally for the three word lengths, respectively. Word frequency was controlled, with an equal number of high- (> 20 times per million) and low-frequency (<20 times per million) words per word length (Kucera & Francis, 1967). The words had a mean word frequency of 52 (SD = 70), with half abstract and half concrete words. This word list has been used previously with alexic patients (Behrmann, Black, & Bub, 1990; Behrmann & McLeod, 1995; Behrmann & Shallice, 1995).

Procedure. Subjects were instructed to read aloud each word as quickly and as accurately as possible. The words were shown individually, with length randomly intermixed in the block of trials. On each trial, a fixation point appeared for 1000msec after which the target word appeared and remained visible until the subject

activated the vocal-response key by reading the stimulus aloud. An interval of two seconds occurred between trials. RT was recorded using a voice key and the experimenter noted any errors. Participants practised on a short list of words, none of which appeared on the subsequent experimental lists. Trials on which the microphone was mis-triggered were removed from the analysis.

Results and Discussion

Repeated measures ANOVAs were performed with group as the between-subject factor, and word length as the within-subject factor. Analyses are done first with accuracy and then with RT. Given the interest in the group differences, throughout, only main effects of group and factors that interact with group are reported.

Accuracy: The Alexia group made significantly more errors than its control group, ($F(1,10)=117.6$, $p<.000$) (mean errors: Alexia 4.4, Controls 0.3), especially as word length increased, ($F(2,20)=3.4$, $p=.05$). The Prosop group also made significantly more errors than its control group ($F(1, 7)=6.8$, $p<.05$) (mean errors: Prosop 2.2, Controls 0.27) but this did not interact with word length. There was no significant difference between the Alexia and Prosop groups in the number of errors and there was no interaction of group x length (both $F<1$).

RT: The data from the two patient groups and their control groups are shown in Figure 2 (note that on this figure, with this y-axis, the data from the two control groups overlap). The Alexia group was significantly slower than its control group, ($F(1,10)=36.5$, $p<.000$), especially as word length increased, ($F(2,20)=52.8$, $p<.000$). The Prosop group was slower than its matched controls ($F(1,7)=120.4$, $p<.000$), especially as length increased, ($F(2.14)=67.8$, $p<.000$). Of note, the Alexia group performed more slowly than the Proso group, ($F(2,10)=6.7$, $p=.04$), and disproportionately so as word length increased, ($F(1,5)=8.96$, $p<.001$). The contrasts between the two patient groups and their controls is clearly evident in the slopes, calculated by regressing RT against word length: whereas the controls for the Alexia and Prosop groups evinced slopes of 5 and 8 ms per additional

letter, respectively, the Prosop patients required 142 ms per additional letter and the Alexia patients required almost four times longer, with a slope of 499 ms per letter.

INSERT FIGURE 2 APPROXIMATELY HERE

Single case comparisons

The data from each patient were compared directly against his/her own matched controls (see Table 2). Here, we examined the slope in RT (as a good summary index) and all seven patients had statistically steeper slopes than their controls, although the Prosop participant, SM, was slightly less affected than the others.

Experiment 1b: Lexical decision

This experiment did not require participants to produce a verbal response and so we adopted it to confirm that the group differences observed above held independent of the requirement for overt articulation.

Methods.

Stimuli. The words from the naming latency task were combined with 60 nonwords, which were created by changing 1 or 2 letters of the real words. All nonwords were pronounceable and orthographically legal; for half the nonwords, the divergence from a real word occurred in the first half of the word whereas the converse was true for the other nonwords. This experiment was run in a separate session from the naming latency task.

Procedure. Following a fixation point that appeared for 1 s, a letter string was presented centrally and remained visible until a key-press was made (again with half-field presentation for the hemianopic alexics and their controls). The inter-trial interval was one second. Subjects decided whether or not the string was a real English word and responded by pressing one of two keys using two fingers of their dominant (right) hand for a "yes" or "no" response. The keys were counterbalanced across subjects. Subjects performed practice trials and

were instructed to complete the task as quickly as possible without sacrificing accuracy.

Results and Discussion.

An ANOVA with string length (3, 5, 7) and type (word, nonword) as within-subjects factors and group as a between-subjects factor was conducted with accuracy and then with RT.

Accuracy: The Alexia group performed significantly less accurately than its control group, ($F(1,10)=11.6$, $p<.01$), especially as string length increased, ($F(2,20)=3.5$, $p<.05$), and no other effects or interactions were significant. The Prosop group's performance did not differ from either their matched controls or from the Alexia group on any factors (all $F<1$).

RT: Mean RTs (and SE), as a function of length, are plotted in Figure 3 for all groups. As evident from this figure, the Alexia group made lexical decisions significantly more slowly than its control counterpart, $F(1,20)=42.2$, $p<.000$), but this was qualified by an interaction with length, ($F(2,20)=17.4$, $p<.000$) and by a three-way interaction of group x length x string type, ($F(2,20)=9.6$, $p<.001$). As revealed by post-hoc Tukey tests ($p<.05$), the three-way interaction emerged because the disproportionate increase in RT with string length was greater for nonwords than for words in the Alexia group, relative to the controls. The Prosop group made lexical decisions more slowly than its matched control ($F(1,10)=67.4$, $p<.000$) and this too was qualified by an interaction with length ($F(2,20)=23.5$, $p<.000$) but this did not interact with string type. The Alexia and Prosop group did not differ significantly in their RT and no interactions were significant (all $F<1$). With regard to the slopes of these RT-length functions, as evident from Figure 3, there was, minimal, if any, change in slope across string length for words and nonwords for the two control groups. There was a moderate cost in RT across length for the Prosop group (slopes 159 ms and 178 ms for words and nonwords) but the slope for the Alexia group was roughly two to three times this for words (342 ms) and far greater for nonwords (639 ms).

Single case comparisons

The single-subject comparisons for the lexical decision compared the slope (across string length for words only) for each patient and his/her matched controls. All patients had significantly steeper slopes than the controls, with SH (Alexia) and CR (Prosop) less affected, relative to their own controls ($p<.05$), than the other patients.

Taken together, the findings from the naming latency and lexical decision tasks confirm that the Alexia patients, all of whom have left occipito-temporal lesions, fit the typical profile of pure alexia: they were slower than their controls, and the increase in RT across word length was disproportionately steep. The Alexia patients also made significantly more errors than their controls, especially towards the ends of words, for example, "trust" for "truck", and "recite" for "recital, and this increased as word length increased. The Alexia patients were also disproportionately slowed, as a function of string length, relative to the Prosop patients, although this was evident only in naming latency, and the number of errors across the two groups did not differ on either task. The novel and most interesting result is that the Prosop patients, all of whom have lesions to the occipito-temporal region of the right hemisphere, were not normal in their orthographic processing abilities, and were significantly slowed in their reading, relative to their own controls. Like the Alexia patients, they were disproportionately slowed as string length increased in both naming latency and lexical decision.

The case study comparisons support the group findings – the Alexia and Prosop patients read aloud and made lexical decisions significantly more poorly than their controls and this was true for each of the individual cases, as well, including the right-hemisphere Prosop patients.

Experiment 2: Face recognition

Experiment 1 revealed that, relative to controls, both the Alexia and Prosop groups were impaired

on word recognition. Experiment 2 explored the complement of this finding, and evaluated the face recognition performance of the patient groups and controls.

Experiment 2a: Simultaneous face discrimination

We documented the speed and accuracy with which the Alexia and Prosop groups and their control groups discriminated between a pair of novel faces. Importantly, we manipulated the difficulty of the discriminability between the faces in the pair, and assess the differential impact of this manipulation. This methodology has been used successfully to examine face discrimination as a function of age (Thomas, et al., 2008).

Methods.

Stimuli. Two novel faces were presented in grey-scale side-by-side on either side of the fixation point (Figure 4a) (for the hemianopic Alexia patients and their controls, the faces were presented entirely to the left of fixation). The faces in the pair could be either identical (25% of trials; N=55) or different (75%; N=165). The different trials could be from Easy, Medium or Difficult conditions (N=55 in each of these levels of difficulty). The Easy condition consisted of a display of two different faces (for example, Face A and Face B). For the medium and difficult trials, the two faces (say Face A and Face B) were morphed together using the MorphMan 4.0 software. For the medium condition, Face A was presented with a second face that was a morph comprising 33% of Face A and 66% of Face B, while in the difficult condition, Face A was presented with a second face that was a morph comprising 66% of Face A and 33% of Face B. Each stimulus was roughly 2 x 3 inches and the midpoint of each stimulus was located 5.2 inches from the fixation point (see Thomas et al., 2008 for more details).

Procedure. Each display was presented for unlimited exposure duration. Participants were informed that, on each trial, two faces would appear, and they were to decide whether the faces were the same or not and to

indicate their response using one of two keys on the keyboard ("D" or "S") as accurately and as quickly as possible. Condition (same, different – easy, medium, difficult) was randomized within a block.

Results and discussion

Accuracy*:* As evident in Figure 4b and summarized in Table 1, the Prosop group made significantly more errors than their controls, ($F(1,7)=8.2$, $p<.05$) and the same was true for the Alexia group relative to their controls, ($F(1,10)=5.8$, $p<.05$). There was no difference in overall accuracy level between the two patient groups ($F<1$). No interactions with difficulty level were observed in any of these ANOVAs presumably because performance in the 'difficult' condition was at or approached chance level for all four groups. To circumvent this floor effect, we re-ran the group analyses using only the 'easy' and 'medium' conditions.

In ANOVA with just the easy and medium levels, there was still a main effect of group for the Prosop vs Controls, ($F(1,7)=7.1$, $p<.05$) and for the Alexia vs Controls, ($F(1,10)=8.8$, $p=.01$). There was no difference in accuracy between the two patient groups, but there was a significant interaction of patient group x condition, ($F(1, 5)=22.1$, $p<.005$). This interaction arose because the groups were equally inaccurate in the medium condition but the Prosop group was less accurate than the Alexia group in the easy condition. Thus, even when the discriminations were fairly easy, the Prosop group performed poorly but, the impairment in the Alexia group was evident only when the faces were somewhat more similar and harder to differentiate.

In light of the fact that the error rates were so high for the difficult condition but also to some extent for the other conditions, we did not analyze the RT data.

Single subject comparison

In these comparisons, we examined the error rate for the patient versus matched control only in the 'easy' condition as this where the Alexia and Prosop patients were maximally differentiable. All of the Prosop

patients performed more poorly than their controls and two of the Alexia patients performed significantly less accurately than their matched controls.

Experiment 2b: Orientation and vantage point in face matching

Having shown that both the Prosop and Alexia groups performed more poorly than their controls (and Prosop more poorly than Alexia in the easy condition), we compared the groups under two well-established and more telling manipulations of face perception: when the faces were presented upright versus inverted and when the faces to be matched were upright but differed in their vantage point.

The upright versus inverted comparison in the two patient groups is of great interest as it has been suggested that prosopagnosic individuals, relative to controls, show an inversion superiority effect, performing better with inverted than upright faces (Farah, Levinson, & Klein, 1995; Farah, Wilson, Drain, & Tanaka, 1998) or, at least, not showing the normal inversion inferiority effect (i.e. equivalent performance for upright and inverted faces) (Avidan, Tanzer, & Behrmann, 2011; Busigny & Rossion, 2010, 2011). This atypical pattern is typically attributed to an impairment in holistic processing in prosopagnosia (Barton, 2009; Barton, Press, Keenan, & O'Connor, 2002), which impairs the ability to extract the configural representation of the face as is standardly done with upright faces. Because inverted faces do not tap into this configural representation and are thought to be processed in a more part-based fashion, the prosopagnosics do relatively better with the inverted than with the upright faces. Examining whether a similar pattern for inverted/upright occurs for the Alexia group might shed light on the computations mediated by each hemisphere.

The assessment of performance across vantage point also serves as a valuable probe of the mechanisms underlying face perception in the Alexia and Prosop groups. We and others have previously established that prosopagnosic individuals perform poorly at matching faces across different vantage points (for example, Marotta, et al., 2002). Examining this ability in the patients with pure alexia may help uncover similarities and differences in the profiles of the two patient groups in face perception performance.

Methods.

Stimuli. The stimuli consisted of color pictures of male and female faces initially collected using a Cyberware™ 3D laser-scanner and collated in the Max-Planck Face Database. This database consists of a series of three-dimensional (3D) models of real faces in three rotations in depth around the vertical axis—full frontal-face (0°), right three-quarter (45°), and right profile (90°) (see Figure 5a-c for examples of the three vantage points). Hair was covered, leaving only the face image. Each face was positioned on a black square background (7.5 cm x 7.5 cm). A total of 97 different faces were used for the experimental trials.

Procedure.

On each trial, three stimuli appeared on a grey background: a target face (centered over fixation, 5.5 cm from the top of the screen) and two choice faces, to the left and right side of the fixation (9.5 cm from left, 16 cm from top) and the other presented on the lower right side of the screen (22.5 cm from left, 16 cm from top) (see Figure 5d and 5e). The two Alexia patients with field defects, and their matched controls, saw all stimuli in the intact left field (although there was unlimited exposure duration and they were free to move their eyes, we still opted for left field presentation to avoid any adverse effect of the hemianopia). Each trial began with a fixation cross appearing for 250 ms, followed by the three stimuli, which remained on the screen until response. In the first part of the study, only upright faces, varying within and across viewpoint, were shown (see example in Figure 5d). The target could appear in one of three possible rotations (frontal, three-quarter and profile) and this was true of the choices too, resulting in nine possible target face x choice faces rotation combinations. Note that, on any one trial, the two choice faces were always rotated to the same angle within a trial, for example both might be 45 degrees, as shown in Figure 5d. The nine conditions were randomly mixed within each block of trials, with 40 trials per cell for a total of 360 trials. Trials were divided into two blocks with a short break between them. Participants pressed a left or right key to indicate the side of the match to target.

Once this viewpoint study was complete, participants completed an additional block of trials, in which the target was always upright and, on half the trials, the choices were both upright while, in the remaining half, the choices were both inverted. The target and choice faces were only ever shown in the frontal plane (see Figure 5e). Participants pressed a left or right key to indicate the side of the match. Again, there were 40 trials per cell (inverted/upright) for a total of 80 trials.

Results and discussion

We describe the effect of orientation on performance first and then present the view change results.

Upright versus inverted

Accuracy: As shown in Figure 6a, the Prosop group made significantly more errors than their matched controls, ($F(1,7)=62.8$, $p<.000$), with disproportionately more errors for upright than inverted faces, as revealed by the group x orientation ($F(1,7)=9.3$, $p=.01$). There were no differences in accuracy between the Alex group and its controls. Lastly, the Prosop group made more errors than the Alexia group, ($F(1,5)=23.5$, $p<.005$) and the interaction of group x orientation condition was marginally significant, ($F(1,5)=5.8$, $p=.06$), with more errors for upright than inverted faces in the Prosop group and no difference across orientation for the Alexia group.

RT: The Prosop group performed significantly more slowly than the controls, ($F(1,7)=10.1$, $p=.01$) although this varied as a function of orientation, ($F(1,7)=6.8$, $p<.04$). As seen in Figure 6b, the Prosop controls showed a slight, albeit non-significant, increase in RT for inverted over upright faces but the Prosop group showed faster RTs on inverted than upright faces ($p<.05$), which mirrors their accuracy data. The Alexia group also performed significantly more slowly than their matched controls, ($F(1,10)=24.9$, $p=.001$), and this too was qualified in an interaction with orientation, ($F(1,10)=4.8$, $p=.05$): unlike the Prosop group, however, the Alexia group showed the same pattern as the controls--- that is, the Alexia patients were slower at inverted than upright trials albeit

to a greater degree than their controls. Finally, there was no main effect of group between the Prosop and Alexia, but there was a significant interaction of group x orientation, ($F(1,5)=21.5$, $p<.01$). Whereas the Prosop group revealed significantly faster RTs for inverted than for upright, the opposite was true in the Alexia group. The interesting and novel finding was that, despite the slowed RTs of the Alexia patients, they continued to evince the advantage for the upright over inverted faces and this contrasts with the inversion superiority seen in the Prosop patients.

Single subject comparisons

For these analyses, we derived a difference score (inverted – upright RT) for each individual and performed the comparison against the matched controls. All seven patients performed more slowly than their controls – each of the Alexia patients (to a lesser degree for DK) was differentially slower than controls, with greater slowing on inverted than upright, whereas for the Prosop patients (to a lesser degree for CR), the reverse was true.

Matching across vantage point

An ANOVA was performed with two within-subject factors: target rotation (frontal, profile and three-quarter) and match rotation (frontal, profile and three-quarter).

Accuracy*:* As evident in Figure 7a, the Prosop group made significantly more errors than its controls, ($F(1, 7)=75.7$, $p<.000$), although this differed as a function of target viewpoint, ($F(2,14)=6.5$, $p=.01$): whereas the controls were most accurate on the three-quarter viewpoint (Bruce, Valentine, & Baddeley, 1987; O'Toole, Edelman, & Bulthoff, 1998), this was not true for the Prosop patients. The Alexia group was as accurate as the matched controls ($F<1$). The Prosop group was significantly less accurate overall than the Alexia group, ($F(1,5)=52.3$, $p<.001$).

RT: As shown in Figure 7b, the Prosop group responded significantly more slowly than the controls, ($F(1,7)=5.5$, $p=.05$), but this varied depending on the target viewpoint, ($F(2,14)=4.7$, $p<.05$): whereas both groups were faster on the three-quarter view relative to the other conditions, this advantage was greater for the Prosop group than the control group presumably because there was greater opportunity for a larger separation in RT between conditions given their slower performance (note also that because of the high error rate for the Prosop patients, the RT data may not be as reliable as one might like). The Alexia group also performed more slowly than its control, ($F(1,10)=22.6$, <.001), and this too was qualified by target viewpoint, ($F2,20)=3.3$, $p=.05$) in the same way as for the Prosop group: there was relatively faster performance for the three-quarter view than the other views in the Alexia group than was true in the controls. There was no significant difference between the Prosop and Alexia groups in overall RT, and, intriguingly, there was no interaction with any other variable indicating the same profile as a function of viewpoint (as can be seen in Figure 7b). Finally, across all these analyses, the vantage point of the choices did not influence performance in any of these comparisons, and only the view of the target affected performance differentially.

Single subject comparison

The single-case analyses were done on the accuracy scores from the profile view – we chose this particular data point both because the Prosop patients were least accurate on this condition and because, as a result of this large error rate, the RT analysis was not feasible. As evident from Table 2, in this condition, all three Prosop patients performed more poorly than their matched controls and two of the four Alexia patients did, as well.

To sum up, we compared the performance of the two patients groups and their controls in matching faces across two manipulations, both of which are known to index competence in face perception: matching across orientation differences (upright versus inverted) and matching across vantage point. In both

accuracy and RT, the Prosops but not Alexia patients were less affected by inversion than their controls. The Alexia group was slower than the controls but the rank ordering of the orientations remained the same although the Alexia group showed greater separation between the conditions.

When considering the viewpoint data, both patient groups performed more slowly than the controls but the patterns were similar: relative to the controls, both groups were disproportionately slowed on the frontal and profile cases with relatively less slowing on the three-quarter views. The Prosop group made more errors than the controls especially on the frontal and three-quarter trials, and more errors overall (but not qualified by viewpoint) than the Alexia group. The Alexia group and controls did not differ in accuracy. Single case comparisons largely supported these group findings.

General discussion

The goal of this study was to examine whether the mechanisms supporting the recognition of visual words and faces are truly independent, as might be predicted on a domain-specific account, or are overlapping, as might be predicted on a more distributed and graded account. While we acknowledge that many neural areas and psychological processes are shared by face and word recognition (for example, early visual cortex and regions engaged in eye movements), the crux of the argument concerns whether there are regions in ventral visual cortex selectively devoted to one or the other visual domain. In addition, to the extent that the mechanisms for faces and words are not independent, as we predict, a further question is whether the neural system that mediates recognition of both of these classes is restricted to a single hemisphere or is instantiated across both hemispheres. To explore these questions, we conducted two series of experiments, one designed to characterize the word recognition abilities, and the other designed to characterize the face recognition abilities, of patients with pure alexia following a lesion restricted to the left hemisphere and of patients with prosopagnosia following a lesion restricted to the right hemisphere. We compared the performance of these groups against each other and against matched controls and, for further analysis, compared each individual patient against his/her own matched controls.

The findings were fairly straightforward: as expected, relative to controls, the pure alexic patients were impaired at word recognition both in speed and accuracy in word reading and in lexical decision. At the same time, the prosopagnosics were slower and less accurate in matching upright and inverted faces (and showed the so-called inversion superiority effect) and also made more errors and were slower when matching only upright faces that differed across viewpoint. We note that these group-level findings also held when the analysis was done at the single patient level.

While the patient groups were clearly impaired in their 'preferred' category, the more telling question concerns their performance in the 'non-preferred' category. Importantly, we observe deficits in both groups here too. The Alexia patients made more errors than their controls on discriminating morphed faces, and performed more slowly on matching upright and inverted faces. Unlike the Prosop patients, however, the Alexia patients showed the exaggeration of the normal upright superiority effect rather than the inversion superiority pattern.

In matching faces across vantage point, the Alexia patients were as accurate as their controls but were slowed, especially for the more taxing frontal and profile views [the three-quarter view is considered easier as more featural information is available; (O'Toole, et al., 1998)]. The Alexia group made significantly fewer errors than the Prosop group on this task, and to a greater degree for profile and three-quarter views, but did not differ in RT. We also note that the individual Alexic patients all performed statistically more poorly on the selected indices for each task than their matched controls, with the exception of DK and SH who did not differ from their controls on the discrimination of morphed faces. In sum, across almost all analyses, the Alexia patients, as a group and as single cases, performed more poorly than their controls on all face tasks, although they were somewhat more accurate and not as slow in RT as the Prosop group.

The complement of this result held for the word recognition performance of the Prosop patients. The Prosop group made more errors than controls in naming latency although not in lexical decision, and were slowed relative to the controls on both tasks, and disproportionately so as string length increased. There was

no difference in error rate between the Prosop and Alexia groups on either word task. There was a substantially steeper slope for the Alexia than Prosop group on single word naming and although this slope difference did not reach statistical significance in lexical decision, there was a large numerical slope difference (Alexia 342ms; Prosop 159ms). All three Prosop patients behaved significantly differently from their matched controls on both word tasks.

These latter analyses reflect the two major novel findings of this study: both patient groups were impaired at both types of stimulus recognition, relative to their controls, but each was impaired to a greater extent in the 'preferred' class relative to the other patient group (Alexia more impaired at word reading than Prosop and Prosop more impaired at face processing than Alexia). In most instances, the pattern of impairment was qualitatively similar in the two groups. Thus, both groups were disproportionately slowed in word reading/lexical decision as a function of string length. That the Prosop patients showed this pattern after a right-hemisphere lesion suggests that the letter-by-letter reading, typically ascribed to left VWFA lesions, applies to right hemisphere lesions too. This result implies that the right VWFA-equivalent might, under normal circumstances, contribute to the parallel letter processing thought to be a function of the left VWFA, and reflects the similarity in the mechanism supporting word recognition in both hemispheres, albeit with greater weight on the left side.

Closer scrutiny of the face recognition data also indicates qualitative similarity across the patient groups although not in all instances. Both patient groups were impaired at discriminating morphed faces although more markedly so in the Prosop than Alexia group. There was, however, a clear qualitative difference between the two groups in their response profile to matching upright versus inverted faces and this may be instructive. Whereas, consistent with many other reports (Farah, Wilson, Drain, & Tanaka, 1998), the Prosop patients performed relatively more accurately on inverted than upright faces, which contrasts with the normal pattern, this was not the case for the Alexia patients who showed the normal pattern albeit in an exaggerated form. One possible account of this difference between the patient groups may be that individual "parts" of visual words can map quasi-systematically to individual phonemes, so perhaps

"holistic" visual processing is not as necessary in the domain of reading as in the domain of face recognition. Presumably local "parts" of faces are not that informative with respect to the identity of an individual person, with the result that mapping from a face percept to other information about the individual requires a more combinatorial/holistic kind of representation. Consistent with this, there is a longstanding proposal that the right hemisphere is more engaged in configural or holistic face representation whereas the left hemisphere is more engaged in featural or elemental representation. A lesion to the right hemisphere essentially removes the ability to represent faces configurally with the result that only featural information is available and this latter ability supports the processing of inverted faces. The left hemisphere lesion in the Alexia group apparently does not impact configural processing and so the pattern of poorer performance with inverted faces is retained. Finally, both groups were impaired at matching faces across changes in viewpoint, again to a greater degree for the Prosop patients than Alexia patients. Because error rate was relatively high in the Prosop group, drawing conclusions based on the RT data is not fully warranted.

As evident, both the Alexia and the Prosop group are impaired relative to each other, depending on the domain, as well as relative to controls. It is the case, however, that almost every patient with brain damage is likely to be somewhat slower and perhaps less accurate on just about any task—and in particular, patients with visual problems are especially likely to be a bit slower and a bit less accurate on any challenging visual task. The question that arises is whether the differences we observe here are simply a general result of the lesion or are specific to the types of processes that mediate face and/or word recognition. The challenge is then to find a domain in which we can establish normal performance for the patients. As laid out in the initial description of the patients, all seven individuals perform within normal limits on finger tapping speed (see Methods) and, thus, they are not ubiquitously slowed in responding. The more telling issue, however, concerns their visual performance. All seven patients perform within normal limits on the spatial tests of the VOSP, further attesting to the fact that their performance is not limited in an across-the-board or general fashion and thus the patterns of perturbation we observe are specific to the mechanisms under investigation, rather than a general consequence of a lesion.

Taken together, these data suggest that even though both hemispheres contribute to face perception, they may do so differentially and a hemispheric division of labor is consistent with ongoing views about different computational roles played by each hemisphere. A review of the neuropsychological literature distinguishes between patients with right hemisphere lesions who show abnormalities in configural coding and those with left hemisphere lesions who are more compromised in the local analysis of the input (Gainotti & Marra, 2011). This finding is also supported by a PET study demonstrating that the right fusiform gyrus was more activated when matching whole faces than face parts whereas this was reversed in the left homologous region (Rossion et al., 2000). Similarly, a recent fMRI study revealed that activation in the right fusiform gyrus correlated with categorical judgments (whether the image was of a face or not) whereas activation in the left hemisphere correlated with image-level face-semblance (Meng, Cherian, Singal, & Sinha, 2012).

The data presented here suggest that pure alexia and prosopagnosia may be homologues of each other, both arising from a lesion to a distributed system that underlies face recognition and word recognition. The emergence of face deficits after left hemisphere lesions and word deficits after right hemisphere lesions clearly indicate participation of both hemispheres in processing both stimulus classes albeit to varying degrees. There is, however, an alternative account that ought to be considered --- that each class is represented solely in one hemisphere, with words on the left and faces on the right, and that a unilateral lesion suppresses the homologous region in the other hemisphere. Thus, for example, the word deficit in prosopagnosia might arise, not because orthography is represented in the right hemisphere, but because the right hemisphere focal lesion that gives rise to prosopagnosia inhibits the activation of the VWFA on the left (and the complement would be true for pure alexia). In fact, a recent imaging study of patient SM, one of the prosopagnosic subjects in the current study, reported that reduced fMRI activation and adaptation to object stimuli in tissue in and around his right-hemisphere lesion were also observed in the homologous regions in his structurally intact left hemisphere (Konen, et al., 2011).

Although we cannot definitively rule out this alternative interpretation, there are particular reasons why it seems implausible in this context. First, Konen et al. (2011) found normal activation in both hemispheres in SM when contrasting objects with fixation, indicating that the mere presence of a unilateral lesion does not suppress contralesional activation per se. Moreover, SM showed reduced neural responses (compared to controls) only for contrasts involving greater perceptual similarity (e.g., objects vs. scrambled objects), with the strongest effect coming from conditions requiring the most precise representational distinctions (e.g., repetition of the same vs. different object). Given the lack of perceptual similarity between faces and words, little if any contralesional suppression would be expected. Nevertheless, a definitive imaging study to examine the response of the intact hemisphere in the prosopagnosic and pure alexic individuals is warranted to definitively rule out this alternative. We already do know that there is bilateral activation for faces and for words in normal individuals [for example, (Hasson, et al., 2002)] but a clearer analysis of the integrity of the activation in the contralesional hemisphere in the patients is warranted.

More generally, though, the Konen et al., (2011) pattern of results is more consistent with a cooperative rather than a competitive (or independent) relationship between homologous regions in the two hemispheres: in the intact brain, the regions interact and support each other in deriving a precise representation of a given stimulus, so that if one is lesioned, the normal support for the homologous region is reduced or eliminated [see (Farah & McClelland, 1991), for a demonstration of this effect within a distributed neural network). By contrast, on a view in which there are unilateral and independent face and word modules, as in a domain-specific account, there is no clear reason why lesioning one should have any effect on the other.

Along these lines, Plaut and Behrmann (2011) have recently articulated a theory, supported by a computational simulation, of how word and face representations become bilaterally but asymmetrically organized as a consequence of specific computational principles and constraints on neural learning (see Johnson, 2011, for a similar, more general developmental perspective). Both word and face recognition rely disproportionately on high-acuity visual information, and due to a topographic bias on learning (to minimize

overall axon volume), their higher-level visual representations both become localized in the fusiform gyrus adjacent to retinotopic visual information from central vision (Hasson, et al., 2002; Levy et al., 2001). Given that the two domains involve incompatible visual primitives, and that word representations need to interact with (typically) left-lateralized phonological and semantic information, competition between the two domains leads to graded hemispheric specialization, with words represented mostly on the left and faces mostly on the right. Plaut and Behrmann (2011) demonstrated in their model that lesions of left-fusiform cortex adjacent to central visual information (analogous to the VWFA) produced a substantial impairment on word recognition but also a milder impairment on face recognition, whereas analogous lesions to right fusiform cortex (analogous to the FFA) produced the opposite pattern. These results are fully consistent with the findings of the current investigation.

A recent empirical study also provides support for this account (Dundas, Plaut, & Behrmann, submitted). This study examined the hemispheric superiority for faces and words in children (7-9 yo), young adolescents (11-13 yo) and adults in a half-field discrimination task. All groups showed a right visual-field advantage for word discrimination, but only the adults showed a reliable left visual-field advantage for face discrimination (even though the adolescents, as a group, were as accurate overall as the adults). Interestingly, the emergence of face lateralization in the younger groups was correlated with reading competence (even after regressing out age and overall face discrimination accuracy). The findings support the view that the hemispheric organization of face and word recognition do not develop independently, and that word lateralization, which emerges earlier, may drive later face lateralization.

Conclusion

Conventional wisdom holds that faces and words are independent domains of high-level vision subserved by independent neural mechanisms located in opposite hemispheres. On this view, lesions to the right hemisphere that impair face recognition (in prosopagnosia) should leave word recognition unaffected, and lesions to the left hemisphere that impair word recognition (in pure alexia) should leave face recognition

unaffected. The current work shows that neither of these predictions is upheld. Instead, prosopagnosics have mild but reliable word recognition deficits, and pure alexics have mild but reliable face recognition deficits. The apparent co-mingling of face and word mechanisms is unexpected from a modular perspective, but follows naturally as a consequence of an interactive, learning-based account in which neural representations for both faces and words are the result of an optimization procedure embodying specific computational principles and constraints.

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Table 1: Summary of ANOVA outcomes for patients versus controls and patient comparisons

	Pairwise group comparison of patients versus controls and of Alex versus Prosop		
Experiment and dependent measure	**Alex versus Controls**	**Prosop versus Controls**	**Alex versus Prosop**
Naming latency			
a. Accuracy	Main effect group; interact with length	Main effect group	No sig. diffs
b. RT	Main effect group; interact with length	Main effect group; interact with length	Main effect group; interact with length
Lexical decision			
a. Accuracy	Main effect group; Interact with length	No sig. diffs	No sig. diffs
b. RT	Three-way interaction: group x length x string type	Main effect group; interact with length	No sig. diffs
Simultaneous face discrimination			
a. Accuracy (3 levels)	Main effect group	Main effect group	No sig. diffs
b. Accuracy (2 levels)	Main effect group	Main effect group	Interaction of group x difficulty
Face matching Orientation effects			
a. Accuracy	No sig. diffs	Main effect group; interact with orientation	Main effect of group; Interaction with orientation
b. RT	Main effect group; interact with orientation	Main effect group; interact with orientation	Interaction of group x orientati
Vantage point			
a. Accuracy	Main effect of group; Interact with target rotation	Main effect of group	Main effect of group; Interact with target rotation
b. RT	Main effect of group; Interact with target rotation	Main effect of group; Interact with target rotatio	No sig. diffs

Table 2: Single case summary statistics (patient versus matched controls)

	Pure alexia				Prosopagnosia		
Experiments	DK^	EL	FF	SH^	SM	RN	CR
Naming latency (RT slope)	**	**	**	**	*	**	**
Lexical decision (RT slope words)	**	**	**	*	**	**	*
Face discrimination (error in 'easy' condition)	n.s	*	*	n.s	**	*	**
Face discrimination (error in 'medium' condition)	*	*	**	**	**	**	**
Face orientation (Inverted – upright difference score)	*	**	**	**	**	**	*
Face vantage point (accuracy in profile view)	*	**	**	*	**	**	**

^ hemianopia

* $p \leq .05$

** $p < .01$

Figure legends:

Figure 1. Representative axial slice from the MRI scan of each of the four pure alexic patients, all showing left occipitotemporal lobe involvement (top row) and a representative slice from the MRI scanof each of the prosopagnosic patients. Details regarding etiology of lesion and time since onset may be found in Methods section.

Figure 2. Mean RT (and 1 SE) for Prosop and for Alex groups, as well as for each of their matched control groups, as a function of word length, for single word naming. The slope, calculated by regressing RT against word length, is included for each group.

Figure 3. Mean RT (and 1 SE) for Prosop and for Alex groups, as well as for each of their matched control groups, as a function of string type and length, for lexical decision. The slope, calculated by regressing RT against string length, is included for each group and for words/nonwords.

Figure 4. (a) Examples of stimuli from the easy, medium and difficult different conditions, and from the same condition. (b) Mean % error rate (and 1 SE) for the Prosop and Alex groups and for their matched control groups for each different condition.

Figure 5. (a-c) Example of a single face stimulus presented in frontal, three-quarter and profile view. (d) Example of an upright trial with the target at the top and the two choices at the bottom; the choice on the left is the correct match. Note that the choices always share the same vantage point and, here, differ from the vantage point of the target. (e) Example of an inverted trial with the target at the top and the two choices at the bottom; the choice on the left is the correct match. Note that the choices were always inverted and the target was always presented upright.

Figure 6. (a) Mean % error (and 1 SE) and (b) Mean RT (and 1 SE) for Alex and Prosop groups and for their matched control groups for upright and inverted face matching.

Figure 7. (a) Mean % error (and 1 SE) and (b) Mean RT (and 1 SE) for Alex and Prosop groups and for their matched control groups for matching faces as a function of vantage point (frontal, profile and three-quarter views).