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Word and text processing in developmental prosopagnosia

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ABSTRACT

The “many-to-many” hypothesis proposes that visual object processing is supported by distributed circuits that overlap for different object categories. For faces and words the hypothesis posits that both posterior fusiform regions contribute to both face and visual word perception and predicts that unilateral lesions impairing one will affect the other. However, studies testing this hypothesis have produced mixed results. We evaluated visual word processing in subjects with developmental prosopagnosia, a condition linked to right posterior fusiform abnormalities. Ten developmental prosopagnosic subjects performed a word-length effect task and a task evaluating the recognition of word content across variations in text style, and the recognition of style across variations in word content. All subjects had normal word-length effects. One had prolonged sorting time for word recognition in handwritten stimuli. These results suggest that the deficit in developmental prosopagnosia is unlikely to affect visual word processing, contrary to predictions of the many-to-many hypothesis.

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The recognition of faces and visual words are highly expert visual processes that are traditionally thought to be independent of each other, in part because of their complementary hemispheric lateralization. Faces produce greater activation in the right hemisphere (Kanwisher & Barton, 2011; Kanwisher, McDermott, & Chun, 1997), while visual words produce greater activation in the left hemisphere (Cohen et al., 2002; Dehaene & Cohen, 2011). Likewise, neuropsychological studies show that prosopagnosia, an impairment of face recognition, is far more common after unilateral right-sided than after left-sided lesions (Atkinson & Adolphs, 2011; Barton, 2008), and pure alexia, a deficit in reading proficiency, usually results from damage in the vicinity of the visual word form area in the left hemisphere (Leff, Spitsyna, Plant, & Wise, 2006; Starrfelt & Shallice, 2014). However, this lateralization is not complete: Neuroimaging studies show, first, that faces and visual words activate bilateral, if asymmetric, networks, and, second, that the regions activated by faces and visual words overlap (Harris, Rice, Young, & Andrews, 2015; Haxby, Hoffman, & Gobbini, 2000; Nestor, Behrmann, & Plaut, 2013).

This overlap between face and visual word activation is a key observation behind the recent “many-

to-many hypothesis” (Behrmann & Plaut, 2013). This hypothesis proposes that visual processing of any one type of object involves not just a single cortical region but a distributed network of regions, and, conversely, any one cortical region may be involved in more than one network and therefore the processing of more than one type of object. Hence processing selectivity is not the property of a specific brain region but emerges from the interaction of a network of regions, each of which may participate in the processing of more than one type of object. In the specific instance of faces and visual words, this hypothesis proposes that the right fusiform cortex, which makes a dominant contribution to face processing, is also involved in visual word processing, while visual word processing areas in the left fusiform region are also involved in face perception. In the neuropsychological context, this leads to the prediction that individuals with acquired prosopagnosia will show at least minor deficits in visual word processing, while individuals with pure alexia will show minor deficits in face processing (Behrmann & Plaut, 2014).

This hypothesis has received some neuropsychological support from a survey of patients with unilateral posterior cerebral arterial infarcts (Gerlach, Marstrand, Starrfelt, & Gade, 2014) and two studies showing face-

processing deficits in alexic subjects (Behrmann & Plaut, 2014; Roberts et al., 2015). Studies of visual word processing in acquired prosopagnosia have produced mixed results, however. One study of three acquired prosopagnosic subjects (Behrmann & Plaut, 2014) examined the word-length effect in reading: that is, the time taken to read a word as a function of the number of its letters, which is an index of the amount of perceptual processing required (Barton, Hanif, Eklinder Björnström, & Hills, 2014). An elevated word-length effect is a classic finding in pure alexia and was also found in these prosopagnosic subjects. However, a second report on 11 subjects found elevated word-length effects only in those subjects with bilateral lesions (Hills, Pancaroglu, Duchaine, & Barton, 2015). A third study found an elevated word-length effect and other signs of impaired reading in only one of five subjects with acquired prosopagnosia (Susilo, Wright, Tree, & Duchaine, 2015). Interestingly, one of these studies found that, instead of impaired visual word processing, almost all prosopagnosic subjects had difficulty perceiving the font or handwriting of text (Hills et al., 2015). It was suggested that these results could fit with the many-to-many hypothesis if the latter incorporated hemispheric specialization for the type of processing being applied to visual text: that is, if the hypothesis allowed for the stylistic aspects of text such as font and handwriting style to be processed in the right hemisphere and the content as it relates to reading to be processed in the left. Thus, it may be that, in terms of processing, it is the operation (e.g., style versus word content of text) rather than the stimulus (e.g., visual words versus faces) that is lateralized.

The goal of the present study was to extend these observations on word and text processing to a group of subjects with developmental prosopagnosia, a life-long impairment in face recognition. The results in a developmental cohort may not parallel those of a group with acquired lesions. Acquired prosopagnosia is often caused by large lesions that affect more than just the face-processing network while subjects with developmental prosopagnosia do not have lesions on standard clinical imaging; hence it is possible that the perceptual impairments of the latter are more closely confined to the face-processing network (Avidan et al., 2014; Garrido et al., 2009; Thomas et al., 2009). This leads to two possible predictions: If the cause of developmental prosopagnosia is a

deficiency of the very resources involved in the competition envisioned in the many-to-many hypothesis, then subtle impairments in reading may be found, even if these are not seen in the acquired group. On the other hand, if these textual properties are processed by adjacent networks rather than by a face-specific network, one might predict that the processing of handwriting or font is more likely to be spared in a developmental cohort.

Method

Subjects

Ten developmental prosopagnosic subjects (three males) with a mean age of 43 years ($SD = 13$, range = 27–66) participated. These subjects had postsecondary education and completed at least 2 years of university courses. All subjects reported life-long difficulty with face recognition as determined by a semi-structured interview, and their face recognition impairment was objectively confirmed with a score at least two standard deviations below the previously reported control mean on the Cambridge Face Memory Task (Duchaine & Nakayama, 2006). Furthermore, each subject had a difference between word and face scores, with faces being worse, in the bottom 5th percentile of the normative data of the Warrington Recognition Memory Test (Warrington, 1984). Finally, all subjects scored in the impaired range on the Twenty-Item Prosopagnosia Index (Shah, Gaule, Sowden, Bird, & Cook, 2015; Table 1). To examine potential perceptual deficits in face processing, subjects also completed the Cambridge Face Perception Task (Duchaine, Yovel, & Nakayama, 2007), and their results were compared to previously published normative data (Table 1).

None of the subjects reported neurological problems or changes in face recognition in their lifetime. All had best corrected visual acuity of better than 20/60, and nine had normal visual fields on Goldmann perimetry and normal colour vision on the Farnsworth–Munsell hue discrimination test (Farnsworth, 1943). (DP032 did not complete Goldmann perimetry or colour vision tests due to time limitations, but reported no vision loss or history of colour blindness.) None had a history of an autism spectrum disorder, and all scored less than 32 on the Autism Questionnaire (Baron-Cohen, Wheelwright, Skinner, Martin, &

Table 1. Demographics and diagnostic tests.

Subject	Age (years)	Gender	CFPT		CFMT	WRMT			PI20	MRI
			Upright	Inverted		Faces	Words	w – f		
Controls mean (<i>SD</i>)			36.7 (12.2)	65 (9.8)	57.9 (7.9)	Based on age	Based on age		38.9 (10.8)	
DP008	61	F	48	96	36	36	49	13	72	yes
DP014	42	M	64	60	32	30	48	18	91	yes
DP016	52	F	48	72	41	37	49	12	87	yes
DP021	29	F	36	80	37	33	50	17	NC	yes
DP024	35	F	62	74	41	38	50	12	75	yes
DP032	66	M	68	84	42	37	47	10	86	no
DP033	46	F	52	82	29	39	50	11	84	contra
DP035	39	M	86	68	32	35	49	14	84	yes
DP038	27	F	32	66	39	36	49	13	91	yes
DP044	36	F	68	82	40	34	49	15	95	yes

Note: Control mean and standard deviations provided based on previously published norms (cited in text). CFPT = Cambridge Face Perception Test; CFMT = Cambridge Face Memory Test; WRMT = Warrington Recognition Memory Test; w – f = words score minus faces score; PI20 = Twenty-Item Prosopagnosia Index; MRI = magnetic resonance imaging; F = female; M = male. contra: MRI was contraindicated or refused due to safety concerns (i.e., metal in the body). NC: Data were not collected because participant was run before PI20 was created. **Bold** values indicate impaired performance.

Clubley, 2001). All except DP014 were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Eight subjects had magnetic resonance brain imaging with T1-weighted and fluid-attenuated inversion recovery (FLAIR) sequences to exclude structural lesions that would have indicated a diagnosis of early acquired prosopagnosia rather than developmental prosopagnosia; magnetic resonance imaging (MRI) was contraindicated in DP033, and DP032 declined imaging because of time limitations (Table 1).

Subjects were administered a battery of standard neuropsychological tests to exclude more general problems of attention [Trail Making Test: A & B (Batterly, 1944), Stars Cancellation Test (Wilson, Cockburn, & Halligan, 1987), Visual Search (Spinnler & Tognoni, 1987)], memory [Wechsler Memory Scale: Word Lists I and II, Digit Span, and Spatial Span (Wechsler, 1997)], and visual-spatial abilities [Hooper Visual Organization Test (Hooper, 1985), Benton Judgment of Line Orientation (Benton, Hamsher, Varney, & Spree, 1983), Visual Object and Space Perception Battery (Warrington & James, 1991), Mental Rotation Task (Grossi, 1991)] (Table 2). In each of these tests, performance was compared to the published normative data included with the measure.

The control group for Experiment 1 consisted of 14 subjects (3 male) with mean age of 30 years ($SD = 13.98$, range = 20–63). Like the experimental group, these subjects had post-secondary education and completed at least 2 years of university courses, except for one whose education stopped after high school. All but one were right-handed. The control group for Experiment 2 consisted of

17 subjects (7 male), with mean age of 38.3 years ($SD = 13.4$, range = 15–59), all right-handed. All control subjects reported normal or corrected-to-normal vision, normal reading, and no history of brain damage, and were paid 10 dollars per hour of participation.

The institutional review boards of Vancouver General Hospital and the University of British Columbia approved the protocol, all subjects gave written informed consent, and the experiment was conducted in accordance with the principles of the Declaration of Helsinki.

Stimuli and procedure

Word-length effect task

This used established stimuli and protocol from prior studies (Bao, Rubino, Taylor, & Barton, 2015; Sheldon, Abegg, Sekunova, & Barton, 2012). Subjects sat 40 cm away from a 21" monitor with a screen resolution of 1024 × 768 pixels and refresh rate of 120 Hz. An Andrea NC-8 microphone (<http://www.andreaelectronics.com>) recorded vocal responses. A headrest and a chinrest stabilized the head. Eye movements were recorded using an Eyelink1000 eye-tracker (www.sr-research.com) with a temporal resolution of 1 ms, a spatial resolution of 0.25°, and sample rate of 1000 Hz. Subjects viewed the screen binocularly, and left eye movements were recorded, except for two subjects for whom the right eye was recorded. Experiment Builder 1.10.1241 was used to present stimuli and record fixations.

Subjects fixated on a central cross, spanning 1.3° of visual angle. When ready, the examiner triggered the

Table 2. Results of the neuropsychological test battery.

Test	Max	DP008	DP014	DP016	DP021	DP024	DP032	DP033	DP035	DP038	DP044
<i>Attention</i>											
Trails A ^a		15	16	18	21	11	24	15	16	20	15
Trails B ^a		29	35	43	46	20	47	31	51	65	42
Star Cancellation	54	54	53	52	52	54	54	52	53	54	54
Visual Search	60	58	56	59	58	59	59	59	55	60	60
<i>Memory (WMS-III)</i>											
Word Lists I Recall TS	19	12	13	8	17	16	17	16	13	17	13
Word Lists II Recall TS	19	14	13	11	12	15	15	15	13	13	15
Digit Span	19	17	14	14	10	14	9	12	16	10	16
Spatial Span	19	12	17	14	6	15	17	12	15	12	18
<i>Visuo-perceptual</i>											
Hooper Visual Organization	30	27	28.5	26	27.5	26.5	23.5	28.5	24	24.5	26.5
Benton Judgement of Line	30	22	30	23	30	24	28	29	28	23	29
<i>Object Perception (VOSP)</i>											
Screening	20	19	20	20	20	20	20	20	20	19	20
Incomplete Letters	20	20	19	20	19	20	20	20	20	19	19
Silhouettes	30	20	14	20	21	22	15	21	20	23	22
Object Decision	20	17	19	17	18	18	18	17	20	19	15
Progressive Silhouettes	20	13	8	10	9	6	7	11	11	11	10
Dot Counting	10	10	10	10	10	10	10	10	9	10	10
Position Discrimination	20	18	20	20	20	20	20	20	19	20	20
Number Location	10	9	10	10	10	10	9	9	10	10	10
<i>Imagery</i>											
Mental Rotation	10	7	10	10	9	10	9	10	10	10	10

Note: WMS-III = Wechsler Memory Scale-Third Edition; VOSP = Visual Object and Space Perception Battery; TS = total score. WMS-III values are reported as scaled scores with a range of 1–19, where the mean is 10 ($SD = 3$). **Bold** values indicate impaired performance based on published normative data.

^aTrails test is scored by number of seconds to completion.

start of a trial with a key press. The cross was replaced by a central dot of 0.9° diameter at the same location. If fixation remained stable within 1° of this dot for 200 ms, a single word appeared centred on the middle of a white screen, composed of black upper-case letters in Arial 35-point font, with height of 1.6° of visual angle per letter. If this fixation criterion was not met within 4 s, calibration was reassessed. The participant read the word aloud as quickly as possible, followed by a second key press to terminate the trial. A microphone recorded the subject's vocal response, and the time between the appearance of the word and the onset of their response was recorded as their response time.

Recordings of each response were reviewed to ensure that reading of the word had triggered the marker for latency. We used an audio editor (Audacity 2.0.5, <http://audacity.sourceforge.net>) to verify the accuracy of the audio file response times reported by Experiment Builder.

There were 140 words, 20 for each of the seven word lengths ranging from three to nine letters. Words were randomly ordered for each subject from a database of 420 words, chosen from the MRC (Medical Research Council) psycholinguistics database (www.psy.uwa.edu.au/MRCDataBase/uwa_mrc.htm). Non-words (i.e., acronyms) and names were removed from the list. The average Kucera–Francis written frequency for

Table 3. Kucera–Francis written frequency.

Word length	Mean frequency	SD	Range
3	1574	8865.58	13–69,971
4	403	1517.58	1–10,595
5	200	580.8	1–3562
6	68	93.67	1–561
7	93	137.27	1–883
8	84	82.96	7–392
9	58	49.91	4–231

Note: Frequency shown as occurrences per million words.

each word length is reported in Table 3, with an overall average frequency of 372 ($SD = 3550$, range = 1–69,971) occurrences per million words. To examine differences in frequency across word lengths, we obtained Welch's adjusted F ratio (Levene's F test revealed that homogeneity of variance was violated), Welch's $F(6, 171.228) = 2.321$, $p = .035$. Post hoc comparisons, using the Games–Howell post hoc procedure for equal variances not assumed, revealed no significant differences between word length pairs.

We averaged all correct trials regardless of word length to calculate an overall mean response time for each subject. To calculate each subject's word-length effect, we obtained the average response time for each word-length condition. The word-length effect is the slope of the regression of these average response times as a function of the number of letters in the word. For both average response time and word-length effect, we first conducted group comparisons,

using independent-samples *t*-tests. We then classified the results of prosopagnosic individuals by comparing their data to the 95% prediction limits obtained from the control data, which is $\mu \pm \{t_{(df, n-1, .025)} \times SD \times \sqrt{[(n+1)/n]}\}$, where μ is the mean of the control sample, *SD* its standard deviation, *n* the number of controls, and *t* the *t*-statistic appropriate for that sample size. This measure tests the hypothesis that an individual subject's score comes from the same distribution as that for the control group (Whitmore, 1986).

Sorting by word versus text style

The word-sorting task from a prior study (Hills et al., 2015) was used. The handwriting stimulus set consisted of 10 words ranging from 2 to 11 letters, each written by 10 different subjects, yielding 100 stimuli. Stimuli were printed in black on white paper and were fixed to 102 × 63-mm cards. The main bodies of these lowercase words were 3–5 mm in height. The computer-font stimulus set consisted of 7 four-letter words, each printed in upper case in eight different styles, yielding 56 stimuli (Figure 1). Font size varied between 16, 18, and 20 point to minimize size cues. All words were printed in black on white paper and fixed to 50 × 60-mm cards. Words were 4–5 mm in height.

The cards for the handwritten set were shuffled and the deck handed to the subject with instructions to sort the cards accurately and quickly into piles of different words, regardless of handwriting. They were timed with a stopwatch. Following this, the 10 cards with the word “maintenance” were placed on the table as exemplars of the 10 different handwriting styles. The subject was now told to sort the remaining cards into piles by handwriting style, rather than word. They were to place each card underneath the “maintenance” exemplar card whose handwriting it most

A *early but go island main-tenance*
 B *plm plum plume plum plumm*
 C HAIR BUNS NICE SOON ZONE
 D EAST EAST EAST EAST EAST

Figure 1. Examples of handwriting and font stimuli. In the handwriting task, subjects were asked to sort cards first by word regardless of the handwriting style, as illustrated by the five examples in Row A, and then by handwriting style regardless of the word, as illustrated in Row B. In the font task, subjects were asked to sort cards first by word (Row C) and then by font style (Row D).

resembled. After placing the card they were not allowed to review it again. A stopwatch measured their completion time. A similar protocol was used for the computer-font set.

Font and handwriting tests were analysed similarly. We calculated a per-item completion time by dividing the time to complete sorting by the number of items in the set. Accuracy for sorting by word content was 100% in all subjects. For sorting by style, we calculated two indices of accuracy. The first was a “fraction correct” measure. The second, a “cluster index”, assessed the randomness of the assignments made by the subject (Barton et al., 2010). We generated contingency tables in which the rows represented the handwriting classification given by the subjects to each card, and the columns represented the actual handwriting style of the card. From the number of cards placed in each pile, we can calculate the expected number of cards in each cell of this table if assortment were random. The square of the difference between the observed and the expected value of each cell was calculated and summed over the entire table to give an uncorrected cluster score, which was then divided by the number of items in the test to give a final “cluster index”. Inability to perceive style would be characterized by more random assignments of cards, resulting in a low value for the cluster index.

As in Experiment 1, we conducted group comparisons with independent-samples *t*-tests. Both of these were corrected for multiple comparisons using the Bonferroni procedure adjusted for inter-test correlations (mean $r = .26$; Sankoh, Huque, & Dubey, 1997): This yielded a *p*-value of .011 for significance equivalent to the $p = .05$ level. We classified the performance of individual subjects according to the 95% prediction limits obtained from the control data. For individual data we performed an age-adjusted analysis by regressing out the variance due to age, and used the residual variance in the function to calculate the 95% prediction intervals appropriate for single-subject comparisons for the regression against age (Liu, Pancaroglu, Hills, Duchaine, & Barton, 2014).

Results

Word-length effect task

Two subjects with developmental prosopagnosia were excluded from this analysis due to an incomplete

data set (DP021) and eye-tracker calibration issues (DP044). Trials were excluded if subjects did not read the entire word correctly. The prosopagnosic group ($M = 140$, $SD = 0$) did not produce any errors and was if anything slightly more accurate than the control group ($M = 137.7$, $SD = 1.82$), $t(20) = 3.523$, $p = .002$.

There were no significant differences in mean response time (Figure 2) between the two groups (developmental prosopagnosia $M = 620.78$ ms, $SD = 100.57$; controls mean = 589.20 ms, $SD = 86.49$), $t(20) = 0.78$, $p = .446$. None of the subjects with developmental prosopagnosia exceeded the 95% prediction limit for reaction time (Table 4).

The word-length effect did not differ between developmental prosopagnosic subjects (mean = 10.38 ms/letter, $SD = 7.85$) and controls (mean = 14.91 ms/letter, $SD = 8.21$); $t(20) = -1.27$, $p = .220$. For individual data, our controls yielded a 95% upper prediction limit of 36.42 ms/letter, which is smaller than the upper limit of 52 ms/letter previously reported in healthy subjects (Sheldon et al., 2012). Nonetheless, even by these more conservative criteria, none of our eight subjects with developmental prosopagnosia had an elevated word-length effect (Table 4).

Sorting by word versus text style

We report first the completion times. For sorting by words, there was no difference between controls and developmental prosopagnosic subjects for either the computer-font stimuli, $t(25) = 2.05$, $p = .05$, or the handwritten stimuli, $t(25) = 0.46$, $p = .65$ (Figure 3). At the individual level, subject DP038 had

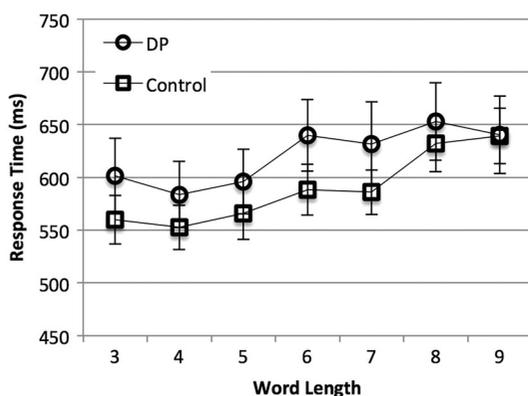


Figure 2. Experiment 1 results: reading time. Word lengths in number of letters are shown on the x-axis, and response time on the y-axis. Error bars represent ± 1 standard error. DP = developmental prosopagnosia.

an elevated completion time for sorting the word content of handwritten but not computer-font stimuli (Table 4).

Completion time for sorting by style did not differ between groups for font, $t(25) = 0.84$, $p = .41$, or handwritten text, $t(25) = 0.20$, $p = .84$. At the individual level, none of the subjects with developmental prosopagnosia showed an elevated completion time for sorting either font or handwritten text by style (Figure 3).

We next report the accuracy data. As in our prior study (Hills et al., 2015), there were no errors by controls or prosopagnosic subjects when sorting either font or handwritten stimuli by word. Accuracy for sorting text by style also did not differ between groups for computer-font, $t(25) = 0.84$, $p = .41$, or handwritten stimuli, $t(25) = 0.52$, $p = .60$. Cluster indices did not differ between groups for either font, $t(25) = 0.79$, $p = .44$, or handwritten text, $t(25) = 0.25$, $p = .80$. At the individual level, none of the subjects with developmental prosopagnosia were impaired (Figure 4).

Discussion

An elevated word-length effect is a hallmark and a diagnostic criterion of pure alexia, a perceptual disorder of reading (Barton et al., 2014). The word-sorting task of Experiment 2 also involves processing the word or orthographic content of a visual text stimulus, but does not require the additional linguistic processes of accessing the mental lexicon or grapheme-to-phoneme conversion that reading aloud does. Rather, it requires extraction of orthographic or word content across variations in style. Thus, these two tasks are complementary probes of visual word perception. Our first result is that only one of our 10 subjects with developmental prosopagnosia (DP038) showed any abnormality on visual word perception: The other nine performed normally on all of our measures of visual word perception. Our second result is that, in contrast to subjects with acquired prosopagnosia (Hills et al., 2015), no subject with developmental prosopagnosia had difficulty with sorting visual text by its stylistic properties.

The many-to-many hypothesis (Behrmann & Plaut, 2013) proposes that the lateralization patterns of both faces and visual words result from competition during the process of learning to read. In particular it proposes that both the right and left posterior

Table 4. Results of word-length effect (Experiment 1) and sorting (Experiment 2) tasks.

	Experiment 1: WLE task		Experiment 2: Sorting by word versus style							
	Mean RT (ms)	WLE (ms/letter)	Font				Handwriting			
			Word sort RT (s/item)	Style sort			Word sort RT (s/item)	Style sort		
Control			RT (s/item)	RT (s/item)	Accuracy	Cluster	RT (s/item)	RT (s/item)	Accuracy	Cluster
95% prediction limits	816	36.4	3.27	12.46	0.39	96	2.54	20.82	0.33	113
Mean (SD)	589 (86)	14.9 (8.2)	1.67 (0.54)	6.29 (2.07)	0.83 (0.15)	194 (33)	1.69 (0.28)	10.28 (3.54)	0.58 (0.08)	311 (67)
Range (min–max)	489–796	3.3–29.3	1.05–2.86	3.77–11.4	0.33–0.98	115–242	1.14–2.15	4.57–16.53	0.44–0.76	220–431
Prosopagnosia										
DP008	578	6.6	1.29	7.96	0.73	165	1.58	11.69	0.69	405
DP014	724	18.2	1.13	7.17	0.83	198	1.55	17.26	0.7	417
DP016	566	8.1	1.34	8.63	0.83	186	1.65	7.23	0.42	221
DP021			1.3	8.29	0.83	198	1.43	7.91	0.51	258
DP024	572	2	0.96	6.42	0.92	222	1.2	13.04	0.56	339
DP032	674	3.9	1.52	6.31	0.6	141	1.54	7.34	0.4	230
DP033	449	3.8	0.93	4.92	0.85	189	1.17	12.42	0.66	375
DP035	638	19.7	1.52	7.25	0.69	144	1.94	11.02	0.43	218
DP038	764	20.8	1.8	6.04	0.88	205	2.71	7.66	0.49	299
DP044			1.21	5.98	0.81	197	1.53	9.9	0.72	417

Note: WLE = word-length effect; RT = reaction time. Accuracy for sorting by word is not included because performance was 100% accurate across groups. **Bold** values indicate impaired performance.

fusiform cortices possess the visual processing resources necessary to individuate stimuli that require high spatial resolution, such as faces or visual words. Learning to read may drive the left posterior fusiform gyrus to become more selective for visual

words, because structural efficiency would favour locating visual word processing near other left-sided areas engaged in language processing (Behrmann & Plaut, 2013, 2015), with the secondary consequence that the right posterior fusiform gyrus becomes more selective for faces. This hypothesis has been supported by studies showing that emergence of

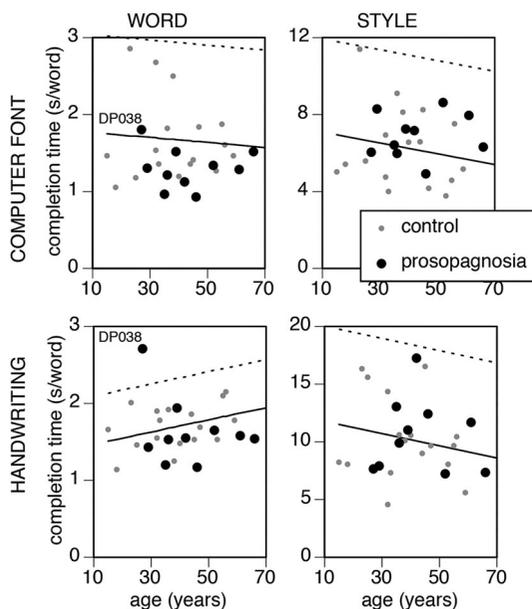


Figure 3. Experiment 2 results: sorting completion time. Times for sorting are plotted as a function of age of subject in all graphs. Left graphs show sorting by word content, and right graphs show sorting by style of text; top graphs show results for computer-font stimuli and bottom graphs for handwritten stimuli. Solid line shows the regression of sorting time against age for controls, with dotted line showing the upper 95% prediction limit of normal performance: Subjects falling above these lines are considered impaired. Only one subject with developmental prosopagnosia had a single prolonged sorting time, for word content in handwriting.

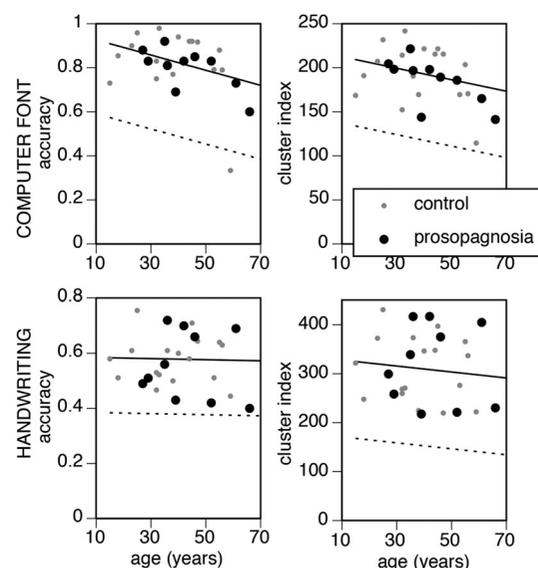


Figure 4. Experiment 2 results: accuracy (left graphs) and cluster index (right graphs) for sorting visual text by style of computer font (top graphs) or handwriting (bottom graphs), plotted against the age of the subject. Solid line shows the regression against age for controls, with dotted line showing the lower 95% prediction limit of normal performance: Subjects falling below these lines are considered impaired. All subjects with developmental prosopagnosia had normal accuracy and cluster indices.

lateralization for not only visual word but also face processing coincides with the onset of reading ability (Dehaene et al., 2010; Dundas, Plaut, & Behrmann, 2013; Ossowski & Behrmann, 2015; Scherf, Behrmann, Humphreys, & Luna, 2007). However, there are also recent data that challenge this: A study using steady-state evoked potentials claims that 6-month-old infants already show right-lateralized face-selective responses (de Heering & Rossion, 2015).

In terms of cognitive models of reading and face recognition, the current anatomic emphasis of the many-to-many hypothesis on the fusiform gyri probably focuses the competition between visual words and faces specifically at perceptual stages. Classic cognitive models of face processing suggest a divergence between the processing of expression- and viewpoint-invariant structural information relevant to facial identity from the processing of dynamic information regarding gaze and expression, followed by interactions of the extracted percept of identity with facial memories and then access to other person-related information (Bruce & Young, 1986; Haxby et al., 2000). Lesion studies in acquired prosopagnosia suggest that the fusiform face area plays a key role in perceptual encoding of facial structure (Barton, Press, Keenan, & O'Connor, 2002), particularly in relation to identity rather than expression (Fox, Hanif, Iaria, Duchaine, & Barton, 2011). Similarly, it is thought that the visual word form area in the left fusiform gyrus participates in the pre-lexical perceptual processing of visual word forms (Dehaene, Cohen, Sigman, & Vinckier, 2005; McCandliss, Cohen, & Dehaene, 2003), extracting letter shapes from combinations of linear and curved elements that then interact with abstract representations of letters and words, followed by access to semantic and phonemic processes. In support, imaging studies show that the left fusiform gyrus is equally responsive to other high-frequency line stimuli such as the scripts of unfamiliar languages and real and pseudo-musical notation (Muayqil, Davies-Thompson, & Barton, 2015), while patients with lesions of the left posterior fusiform gyrus have not only alexia but also deficits in processing chequerboards and unfamiliar scripts (Roberts et al., 2013). Less is known about the extraction of font and handwriting. This shares with visual word processing an analysis of high-spatial-frequency line segments, rather than the complex three-dimensional surfaces of faces. However, while extracting letter identities

independent of style involves detecting specific combinations of lines and curves, while properties such as slant and aspect ratio are treated as noise, this is reversed in the process of identifying style independent of orthographic content. In addition to the studies of acquired prosopagnosic subjects described above (Hills et al., 2015), there is neuroimaging evidence of sensitivity of the fusiform gyri to handwriting style (Barton, Fox, Sekunova, & Iaria, 2009).

The many-to-many hypothesis generates testable predictions in neuropsychological populations, particularly when damage involves the posterior fusiform gyri. As outlined in the introduction, the evidence so far is mixed. First are two recent surveys of patients with posterior cerebral arterial infarcts. One applied a large battery of short tests to 31 patients with unilateral posterior cerebral arterial infarcts (Gerlach et al., 2014). Patients with either right or left lesions made errors on the reading of 10 words, the recognition of 20 famous faces, or the recall of five recently seen faces. In addition, accuracies in reading and making gender decisions in a chimeric faces task were correlated in those with right-sided but not in those with left-sided lesions. A second survey of 31 patients with more chronic posterior cerebral infarcts (Martinaud et al., 2012) used more detailed tests. Three of five patients with lesions in the vicinity of the left visual word form area showed reading impairments: Of these, one was also impaired in face detection and short-term familiarity for faces but the other two were not. As a group, patients with left-sided lesions did well on detection and short-term memory for faces. Patients with right-sided lesions had difficulty with similar tasks for most object types, including detection of visual words, but did not show reading impairments.

Second are studies of face perception in alexic subjects. One study of four patients found impaired same-different judgments about facial identity and slow but accurate matching of faces across viewpoint changes (Behrmann & Plaut, 2014). A second study of 19 patients found slow but accurate matching of famous names to faces and reduced efficiency in same/different judgments about the spatial configuration of facial features (Roberts et al., 2015). On the other hand, two studies have reported a dissociation between face and visual word processing in pure alexia. Three alexic subjects had intact familiarity and occupational categorization of famous faces, apart

from slightly longer reaction times for occupation categorization in one (Purcell, Shea, & Rapp, 2014; Tsapikini & Rapp, 2010), and a large battery of tests on subject C.K. indicated intact recognition of upright faces (Moscovitch, Winocur, & Behrmann, 1997).

Also equivocal are the results from the third approach, the study of visual word perception in prosopagnosic subjects. Three reports on acquired prosopagnosia have examined the word-length effect. One found elevated word-length effects in three subjects (Behrmann & Plaut, 2014), but as others have pointed out (Hills et al., 2015; Susilo et al., 2015), interpreting these data is complicated by the fact that the subjects have been described elsewhere as having an integrative agnosia (Behrmann & Kimchi, 2003). On the other hand, two studies have demonstrated a dissociation between visual word and face processing in acquired prosopagnosia. While elevated word-length effects were demonstrated in four subjects with prosopagnosia after bilateral lesions, five subjects with prosopagnosia after right anterior temporal or right fusiform lesions showed no evidence of reading impairment (Hills et al., 2015). Similarly, word-length effects in lexical decision and reading aloud tasks were evaluated in five subjects with acquired prosopagnosia, four with unilateral lesions and two with fusiform lesions: Only one subject had consistent problems (Susilo et al., 2015).

Our results in developmental prosopagnosia are consistent with as-yet unpublished data from another study of 10 subjects with this condition (Starrfelt, Klargaard, Petersen, & Gerlach, 2015; 2016). This found normal reading latency, normal word-length effects, and normal paragraph reading speeds. It also showed normal word-superiority effects, the ability to identify letters faster when they are embedded within words, which provides evidence that subjects with developmental prosopagnosia are not using a letter-by-letter strategy to read.

What are the implications of relatively normal visual word perception in developmental prosopagnosia for the many-to-many hypothesis? The specific neuropsychological prediction of this hypothesis, as it relates to the right fusiform gyrus, is that because activations from visual words and faces overlap in this cortical region, this region may participate in both visual word and face processing, and hence damage to the right fusiform gyrus would not only impair face perception, leading to prosopagnosia, but also impair

the reading of visual words, at least to some degree. The finding that visual word reading is intact in developmental prosopagnosia thus represents an important challenge to the many-to-many hypothesis. However, the derivation of the neuropsychological prediction from the hypothesis is contingent upon at least three assumptions, and it is possible that it is one of these three assumptions rather than the hypothesis that is not valid.

The first assumption concerns the anatomic extent of the resource competition between the networks for visual words and faces, and how this relates to the locus of the problem in developmental prosopagnosia. Attention has focused mainly on the overlap of activation in the fusiform cortex (Harris et al., 2015; Nestor et al., 2013), but the processing networks extend to middle or superior temporal and inferior frontal regions too, among others, and at some point the networks for faces and visual words must diverge, with visual words integrating into linguistic networks and faces linking to people-semantic networks. The first assumption is that developmental prosopagnosia arises from an anomaly at a stage where face and visual word processing overlap anatomically and have not yet diverged. However, if developmental prosopagnosia is due to an anomaly affecting the face network at a point after visual word and face processing have diverged, the prediction is that there would be intact reading ability in these subjects.

The second assumption is related and follows naturally from this first point and the current focus on overlap between visual word and face processing in the fusiform gyrus. This is that developmental prosopagnosia is due to some anomaly involving the fusiform gyrus. Some find subtle abnormalities in the activation or structure of the right posterior fusiform gyrus (Furl, Garrido, Dolan, Driver, & Duchaine, 2011; Garrido et al., 2009; Hadjikhani & de Gelder, 2002; Song et al., 2015). Others find normal activation of the fusiform face area and other components of the core face network (Avidan et al., 2014; Thomas et al., 2009), which may be consistent with other studies that report abnormal connectivity with more anterior temporal structures (Avidan et al., 2014; Gomez et al., 2015; Thomas et al., 2009). Which view is correct is not yet certain, and of course there is always the possibility that, like acquired prosopagnosia (Davies-Thompson, Pancaroglu, & Barton, 2014),

developmental prosopagnosia is structurally heterogeneous. Thus, if the fusiform gyrus is the main locus of resource competition between visual words and faces, one would predict that developmental prosopagnosic subjects with fusiform anomalies will have visual word processing problems while those with structural abnormalities elsewhere will have normal visual word processing. Hence one must be cautious about the implications of normal reading in developmental prosopagnosia for the many-to-many hypothesis until more is known about which components of the face-processing network are dysfunctional in this disorder. In this regard, evidence of normal visual word processing in subjects with acquired prosopagnosia from unilateral right fusiform lesions (Hills et al., 2015; Susilo et al., 2015) is a more significant challenge to the many-to-many hypothesis.

The third assumption is a functional one, that damage to the right fusiform region activated by visual words would lead to impaired reading. However, activation of a region by visual words on neuroimaging does not necessarily mean that the region makes a critical contribution to visual word processing, and that this will be manifest as a reading deficit if that region is lesioned. Whether a reading deficit emerges depends upon what type of processing occurs in the different regional components of face and visual word networks, and in particular how this differs between the hemispheres. As others have remarked (Gerlach et al., 2014), it is not known whether the processing contributions of right- and left-sided regions are equivalent, redundant, or different. If equivalent, this means that both the right and left fusiform regions make essential and non-redundant contributions to both face and visual word processing. That is, both regions participate in the same processes for face and word recognition, and one cannot compensate completely for the other. It is this first scenario upon which the prediction of impaired visual word processing in prosopagnosia from right fusiform lesions is based. However, in the second scenario, if the right fusiform gyrus does participate in visual word processing but its contribution is redundant to the major contribution of the left fusiform gyrus, then loss of its visual word processing would not be evident as long as the left hemisphere was intact. Finally, both left and right fusiform regions may be involved in processing visual text, but make different contributions to different kinds of

processing of text. For visual text, there have been anecdotal observations that handwriting perception seemed intact in alexic patients with left-sided lesions and impaired in a prosopagnosic patient with a right-sided lesion (Alajouanine, Lhermitte, & de Ribaucourt-Ducarne, 1960; Campbell, Landis, & Regard, 1986; Landis & Regard, 1988; Rentschler, Treutwein, & Landis, 1994). This was confirmed by objective testing in one alexic and three prosopagnosic subjects (Barton et al., 2010), and the results in acquired prosopagnosia were extended to a larger cohort, showing impaired perception of font or handwriting in 10 of 11 subjects, including five with unilateral right-sided lesions (Hills et al., 2015). This suggests a concept of visual text as a multi-dimensional stimulus whose processing involves complementary, non-redundant hemispheric contributions, with the left extracting language-related aspects (i.e., words) of text stimuli—that is, what does it say—and the right stylistic properties such as handwriting and font—that is, who wrote it. If the anomaly in developmental prosopagnosia is limited to right-sided components involved in face perception, this view of different complementary contributions of the right and left fusiform gyri to visual text processing could account for the intact reading ability of these subjects, even if visual text activates regions that overlap with the face network on the right.

However, in the current study none of 10 subjects with developmental prosopagnosia were impaired in processing the stylistic properties of text, which contrasts with the high frequency of such impairments in acquired prosopagnosia (Hills et al., 2015). One possible reason for this difference is that the impairment in developmental prosopagnosia is less severe than in the acquired form. Indeed, a comparison of performance on the Cambridge Face Memory Test of the two groups shows lower scores for those with acquired lesions ($M = 30.7$, $SD = 6.7$) than for those with the developmental form ($M = 36.9$, $SD = 4.5$), $t(9) = 2.64$, $p < .025$. A second possible reason arises if textual style and faces are processed by parallel adjacent circuits rather than the same network. The lesions in acquired prosopagnosia tend to be large, like most naturally acquired pathology, and it is improbable that they affect only face-processing regions. Damage to adjacent cerebral areas probably account for the frequent association of dyschromatopsia and field defects with prosopagnosia, for example, deficits

that do not occur in developmental prosopagnosia. If the anomaly in developmental prosopagnosia is more face selective, this could account for better preservation of the processing of textual style and other visual functions in that cohort.

Finally, we would like to discuss a point made by Susilo et al. (2015), regarding the possibility that the competition for resources in the posterior fusiform cortex between visual words and faces may occur primarily in the left hemisphere. Demonstrations of increasing word superiority and decreasing face responsiveness in the left hemisphere coinciding with the onset of reading (Dundas et al., 2013; Ossowski & Behrmann, 2015; Scherf et al., 2007) may be evidence of such competition on the left, but the lack of a complementary result in the right hemisphere is curious and may suggest that competition between visual words and faces is more muted or possibly non-existent on the right. If so, the prediction would be highly selective deficits for faces and not visual words after right fusiform damage, but less selective deficits that affect both visual words and faces after left fusiform damage. Indeed, the most consistent neuropsychological results so far are modest deficits in face processing among alexic subjects, while visual word processing deficits are difficult to find in prosopagnosia. Against this, though, are findings that suggest more frequent deficits of both visual word and face processing after right- than left-sided lesions following unilateral occipital infarcts (Gerlach et al., 2014). Nevertheless, this would be another potential explanation of the normal visual word processing seen in studies of developmental and acquired prosopagnosia.

Thus, the present data establish normal visual word processing in the majority of the subjects with developmental prosopagnosia that we studied. Only one subject, DP038, was slow on sorting handwritten words by the word. She also had the longest reading time and word-length effect of the prosopagnosic group, although her results still fell within the normal range. This is not simply because her underlying perceptual problem is more severe than the other prosopagnosics: Her scores on the Cambridge Face Memory Task and Cambridge Face Perception Task were in the middle range for the cohort. While one might query a mild subclinical reading anomaly in DP038, it is clear that the rest of the subjects do not show any problem with visual word processing.

This adds to a growing body of studies showing intact visual word processing in many cases of acquired and developmental prosopagnosia. While this contradicts a prediction derived from the many-to-many hypothesis, we have discussed how this prediction is based upon a number of structural and functional assumptions about the role of the right fusiform gyrus in processing visual text and the locus of the defect in developmental prosopagnosia in relation to visual word and face-processing networks. Our results may not invalidate the hypothesis, but rather some of the assumptions upon which the hypothesis is predicated. At minimum, our findings indicate that further refinements are needed to the many-to-many hypothesis, which still represents an important and testable account of visual hemispheric specialization.

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