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Hemispheric organization in disorders of development

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ABSTRACT

A recent theoretical account posits that, during the acquisition of word recognition in childhood, the pressure to couple visual and language representations in the left hemisphere (LH) results in competition with the LH representation of faces, which consequently become largely, albeit not exclusively, lateralized to the right hemisphere (RH). We explore predictions from this hypothesis using a hemifield behavioural paradigm with words and faces as stimuli, with concurrent event-related potential (ERP) measurement, in a group of adults with developmental dyslexia (DD) or with congenital prosopagnosia (CP) and matched control participants. Behaviourally, the DD group exhibited clear deficits in both word and face processing relative to controls, while the CP group showed a specific deficit in face processing only. This pattern was mirrored in the ERP data too. The DD group evinced neither the normal ERP pattern of RH dominance for faces nor the LH dominance for words. In contrast, the CP group showed the typical ERP superiority for words in the LH but did not show the typical RH superiority for faces. These findings are consistent with the hypothesis that the typical hemispheric organization for words can develop in the absence of typical hemispheric organization for faces but not vice versa, supporting the account of interactive perceptual development.

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Prosopagnosia; N170; developmental dyslexia; face recognition; word recognition; hemispheric organization

An ongoing debate that plagues researchers in visual neuroscience concerns the functional organization of the brain processes that underlie the recognition of different visual inputs. One recent theoretical perspective concerning the hemispheric organization of processes that subserve visual recognition (Behrmann & Plaut, 2015) suggests that, rather than being entirely segregated, both the left hemisphere (LH) and the right hemisphere (RH) are implicated in the processing of both word and face representations albeit with weighted asymmetry, with greater activation for words in the LH and for faces in the RH. Many neuropsychological and neuroimaging studies provide empirical support both for the bilateral hemispheric correlates for both stimulus types, as well as for the dominance of word and face representations in their respective hemispheres (Behrmann & Plaut, 2014; Harris, Rice, Young, & Andrews, 2016; Hasson, Levy, Behrmann, Hendler, & Malach, 2002; Roberts et al., 2015; Woodhead, Wise, Sereno, & Leech, 2011).

Co-development of word and face processing

An obvious question concerns the origin of this pattern of graded bilateral hemispheric organization for words and faces. The theoretical account mentioned above addresses this specifically and proposes that this organization results from the interdependence in the development of hemispheric organization for words with that for faces in childhood. Specifically, the hypothesis is that both word and face recognition require high-acuity visual discrimination of homogeneous exemplars and, as such, engage that portion of the visual system (the anterior extrapolation of fovea into extrastriate cortex) that allows for maximum visual acuity of complex patterns (Hasson, Harel, Levy, & Malach, 2003; Levy, Hasson, Avidan, Hendler, & Malach, 2001). During the course of acquiring word recognition skills, the pressure to couple visual and language representations while minimizing axonal length tunes this region of the LH to the statistics of the individual's orthography

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(Baker et al., 2007). As a result, by virtue of competition for cortical representation, the representations of faces become largely, albeit not exclusively, lateralized in the RH.

Evidence from developmental studies supports the assertion that face and word processing develop together as a function of emerging literacy. An investigation using a half-field presentation of faces and words revealed that whereas adults show the expected behavioural superiority when words were presented in the right visual field (RVF) compared with the left visual field (LVF) and the expected behavioural superiority when faces were presented to the LVF compared with the RVF, adolescents and younger children evinced only the former but not the latter asymmetry (Dundas, Plaut, & Behrmann, 2012). Moreover, across the sample of participants, the more competent the reading performance, the greater the RH advantage for face processing, reflected as the accuracy for face discrimination in the LVF over the RVF. These findings led to the conclusion that, during the course of learning to read, word recognition results in a gradual coupling of LH visual and language areas (reflected in RVF over LVF superiority) with the result that, through LH competition, face recognition is shifted to be more, albeit not exclusively, RH mediated (for related ideas and evidence, see Cantlon, Pinel, Dehaene, & Pelphrey, 2011; Dehaene, Cohen, Morais, & Kolinsky, 2015).

Further support for this account was obtained in a subsequent event-related potential (ERP) study (Dundas, Plaut, & Behrmann, 2014) in which, perhaps unsurprisingly, with increased reading experience, children began to show the classic ERP finding of LH N170 in response to single words, corroborating similar earlier evidence (Brem et al., 2010; Maurer et al., 2006). The more novel result was that, concurrent with the lateralization of the N170 to the LH for words, the RH N170 selectivity for faces began to emerge, although reliable adult lateralization patterns were not evident until adolescence.

Together, these findings suggest that the development of word processing and the development of face processing are interdependent processes that draw on overlapping neural mechanisms. An obvious prediction from this account follows: if there is no a priori lateralization and the trigger for lateralization arises from the pressure to learn to read and the ensuing connectivity between the LH

visual and language areas, then, any process that affects the acquisition of reading skills might not only affect word recognition but might also have adverse consequences for the lateralization of face recognition. One underlying mechanism may involve competition in the LH, as neurons in the visual pathway become more tuned for words, driving correlative neural tuning in the RH for faces, albeit not exclusively in each respective hemisphere. A consequence of this process may be poor lateralization for both words and faces as a result of atypical word reading acquisition.

Disturbance in reading acquisition and lateralization effects

Consistent with the prediction laid out above, there is growing recognition that individuals with developmental dyslexia (DD) have atypical LH neural correlates for reading (and perhaps atypical cerebral lateralization more generally, see Bishop, 2013, for review) and that the impairment may not be restricted to reading but may also affect the perception of faces.

Many studies have documented an atypical neural profile in DD as revealed by the reduction in blood oxygen level dependent (BOLD) signals in left extrastriate cortex (Langer, Benjamin, Minas, & Gaab, 2013; Maisog, Einbinder, Flowers, Turkeltaub, & Eden, 2008; Pugh et al., 2000; Wandell, Rauschecker, & Yeatman, 2012), lower amplitude magnetoencephalography (MEG) signals in the vicinity of the left inferior occipitotemporal cortex (Salmelin, Kiesilä, Uutela, Service, & Salonen, 1996), as well as changes in grey-white matter proportion and in the integrity of white matter tracts in these same regions (see Richlan, Kronbichler, & Wimmer, 2013; Wandell et al., 2012).

Evidence for a concurrent impairment in face perception is provided by the finding that a well-characterized group of DD adults performed significantly more poorly compared with controls (Sigurdardottir, Ívarsson, Kristinsdóttir, & Kristjánsson, 2015) on the Cambridge Face Memory Test (Duchaine & Nakayama, 2006). Similarly, relative to controls, DD individuals matched faces more slowly, showed disproportionate cost in performance when target and distractor faces differed in viewpoint, and discriminated faces more poorly, particularly as the faces were increasingly alike perceptually (Gabay, Dundas, Plaut, & Behrmann, 2017). Interestingly, the same DD adults did not show

abnormal performance when required to match cars, ruling out a general visual processing deficit as the basis of the concurrent word and face impairment. The neural profile of DD individuals in response to face stimuli is also atypical: whereas children with dyslexia show normal responses to houses and checkerboards, relative to controls, they evince reduced activation to words in the visual word form area (VWFA) and to faces in the fusiform face area (FFA) (Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012).

Together, these findings are consistent with the presence of a deficit in face perception in DD and, more generally, with alterations in the neural profile of the LH. There has not, however, been a study that directly examines the hemispheric organization of faces and words in this population. As noted, the prediction is that if word-reading acquisition serves as the impetus for hemispheric specialization for visual stimuli, then DDs should evince atypical hemispheric lateralization for both words and faces.

Disturbance in face recognition acquisition and lateralization effects

Unlike DD, in which the developmental difficulty in word acquisition is predicted to affect face lateralization (as words serve as the trigger for lateralization), we hypothesize that there should not be any effect of altered word recognition in individuals who experience difficulty in learning to recognize faces. The candidate population to evaluate such a prediction is that of individuals with congenital prosopagnosia (CP), a developmental deficit in face recognition (colloquially referred to as “face blindness”). Unlike patients with the acquired form of prosopagnosia, who have typically sustained frank brain damage, usually to the right ventral occipital region, possibly even in childhood (e.g., Farah, Rabinowitz, Quinn, & Liu, 2000), those with CP exhibit a face processing deficit in the absence of any obvious frank neurological damage.

The claim is that the CP deficit in face processing may arise separately from the acquisition of word recognition, perhaps due to an underdeveloped inferior longitudinal fasciculus (Thomas et al., 2009), connecting anterior and posterior regions of the RH face processing network (Rosenthal et al., 2017). The deficit may become more pronounced as word reading acquisition comes online, tuning LH visual processing

areas for words. Thus, any abnormality in face recognition may arise but have no effect on the preceding organization of word recognition.

CP is, therefore, likely the result of an errant developmental trajectory in the mastery of face recognition, perhaps akin to the mechanisms that give rise to DD (Klingberg et al., 2000; Richlan et al., 2013; Thomas et al., 2009). Indeed, recent evidence has already shown that, at least in the behavioural domain, CPs do not exhibit word processing difficulties (Burns et al., 2017; Rubino, Corrow, Corrow, Duchaine, & Barton, 2016; Starrfelt, Klargaard, Petersen, & Gerlach, 2017) providing at least behavioural support for the described hypothesis.

Although there is no fully agreed-upon profile for CP (or even a gold standard for diagnosis yet), the inability to recognize faces of well-known individuals (family, friends, famous individuals) is probably the defining characteristic (Geskin & Behrmann, 2017). The deficit may extend beyond recognition, however: while CP individuals appear able to detect the presence of a face in a display and identify the age, sex, or emotion of the face (e.g., Dalrymple, Garrido, & Duchaine, 2014; Garrido, Duchaine, & Nakayama, 2008; Humphreys, Avidan, & Behrmann, 2007; Nunn, Postma, & Pearson, 2001), they may have difficulties in matching novel faces, especially across changes in viewpoint (Avidan, Hasson, Malach, & Behrmann, 2005; Bentin, Degutis, D’Esposito, & Robertson, 2007; Duchaine, Parker, & Nakayama, 2003) or orientation (Behrmann, Avidan, Marotta, & Kimchi, 2005; Schmalzl, Palermo, Harris, & Coltheart, 2009). To our knowledge, no study has characterized the hemispheric organization of words and faces in individuals with CP.

The current study

In this paper, we examine both of the predictions set out above by comparing and contrasting the hemispheric organization of a group of adult individuals with DD and a group of adults with CP, and we examine their profiles in relation to that of a group of control individuals. We conduct these comparisons using behavioural and electrophysiological measures and, in so doing, contribute to our understanding of the neural correlates of the face recognition deficit in CP, the word recognition deficits in DD, and the origins of hemispheric organization. Importantly,

equating word and face stimuli in visual processing experiments is exceptionally difficult. Consequently, all contrasts of interest compare the response to faces between hemispheres or visual fields, and, separately, the response to words between hemispheres or visual fields. We specifically predict that, in normal individuals, faces have a processing advantage in the LVF/RH compared to the RVF/LH, while words have the advantage in the RVF/LH compared to the LVF/RH. The theory described above specifically predicts that DDs will not show this advantage for either stimulus type, while CPs will show that advantage for words, but not faces.

Materials and methods

Participants

All participants were native English speakers and were right-handed, as assessed by Edinburgh Handedness Inventory (Oldfield, 1971). All had normal or corrected-to-normal vision, and had no history of neurological or psychiatric trauma or injury. Participants consented to participate under the protocol approved by the Institutional Review Board at Carnegie Mellon University. They were compensated US\$25 per hour and the experiment took approximately 90 minutes.

The participants fell into three groups:

- (a) CP: Seven participants (six females, Age = 44.6, $SD = 6.61$) met criteria for CP (Table 1), reporting life-long difficulties in face recognition. The CPs performed at least 1.5–2 standard deviations below average on the Cambridge Face Memory Test. Additionally, we assayed face recognition in a task in which photographs of famous individuals such as Hillary Rodham Clinton and Oprah Winfrey (randomly interleaved with photographs of individuals famous in Russia, who should be unknown to all participants) were shown for identification. Again, the CP individuals again fell at least 1.5–2 standard deviations below the mean of the control observers.
- (b) DD: The 10 DD individuals (eight females, Age = 26.2, $SD = 10.9$) were all native English speakers and university students. A well-documented history of dyslexia constituted the key inclusion criterion for the DD group: (1) each individual received a formal diagnosis of DD by a qualified psychologist prior to inclusion in this study; (2) each individual's diagnosis was verified by the diagnostic and therapeutic centre at their university and each was receiving accommodations appropriate to their educational setting. Additionally, participants completed untimed and timed (fluency) tests of Word Identification (WI) and Word Attack (WA) subtests from the Woodcock Reading Mastery Test-Revised, and the Sight Word Efficiency Forms A + B (i.e., rate of WI) and Phonemic Decoding Efficiency, Forms A + B (i.e., rate of decoding pseudo words) subtests from the Test of Word Reading Efficiency (TOWRE-II; Torgesen, Wagner, & Rashotte, 1999). Compared with the control group, the DD group showed a clear profile of reading disability, with significant group differences on word reading and decoding skills, as evident on both rate and accuracy measures, and characteristic deficits of reading difficulties, as manifest in phonological awareness (spoonerisms) and rapid naming (rapid automatized naming) tasks. These participants come from a larger group of 15 DDs with education and age matched controls, summarized in Table 2 (for more details, see Gabay et al., 2017).
- (c) Controls: These 22 individuals (17 females, Age = 25.2, $SD = 2.42$), none of whom had face or word recognition difficulties, served as typically developed controls (TD).

Table 1. Participant demographic information. Metrics for handedness, CFMT, and Famous Faces were taken from Oldfield (1971), Duchaine and Nakayama (2006), and Avidan and Behrmann (2008), respectively.

CP	Sex	Age	Handedness (Oldfield)	CFMT (z-score)	Famous Faces (z-score)
WA	F	26	+84	40 (−2.58)	89.3 (0.39)
KG	F	49	+95	33 (−3.50)	75 (−0.69)
BQ	F	30	+100	30 (−3.89)	19.6 (−4.88)
SC	M	65	+100	46 (−1.79)	64.3 (−1.50)
BL	F	21	+100	28 (−4.16)	23.2 (−4.61)
MN	F	54	0	52 (−1.00)	58.9 (−1.91)
OD	F	67	+95	29 (−3.2)	30 (−3.67)

Importantly, all participants are current university students or degree holders (several in each group from Carnegie Mellon University), none of whom endorsed any cognitive deficit beyond those specific to their diagnostic group (e.g., face deficit for CPs; reading deficit for DDs). Therefore, differences between groups are unlikely to result from difference in general intelligence or other measures of cognitive ability.

Table 2. Demographic and psychometric data (means) of DD and matched control groups from Gabay et al. (2017).

Measure	Group		<i>p</i>
	DD	Controls	
Age (in years)	21.54	22.63	n.s.
Ravens	56.45	58.18	n.s.
Digit span ^a	10.9	13.5	<.05*
RAN objects ^a	103.45	117.45	<.05*
RAN colours ^a	100.09	110.45	<.05*
RAN numbers ^a	106.90	114.18	<.01**
RAN letters ^a	103.54	112.27	<.01**
WRMT-R WI ^a	99.81	113.72	<.01**
WRMT-R WA ^a	98.72	115.63	<.01**
Towre SA (A + B) ^a	100.09	113.81	<.01**
Towre PD (A + B) ^a	91.36	115.45	<.01**
Spoonerism time	132.09	95.81	<.05*
Spoonerism accuracy	8.45	11.27	<.05*

p* < .05.*p* < .01.^aStandard scores, other are raw scores. Numbers represent means.

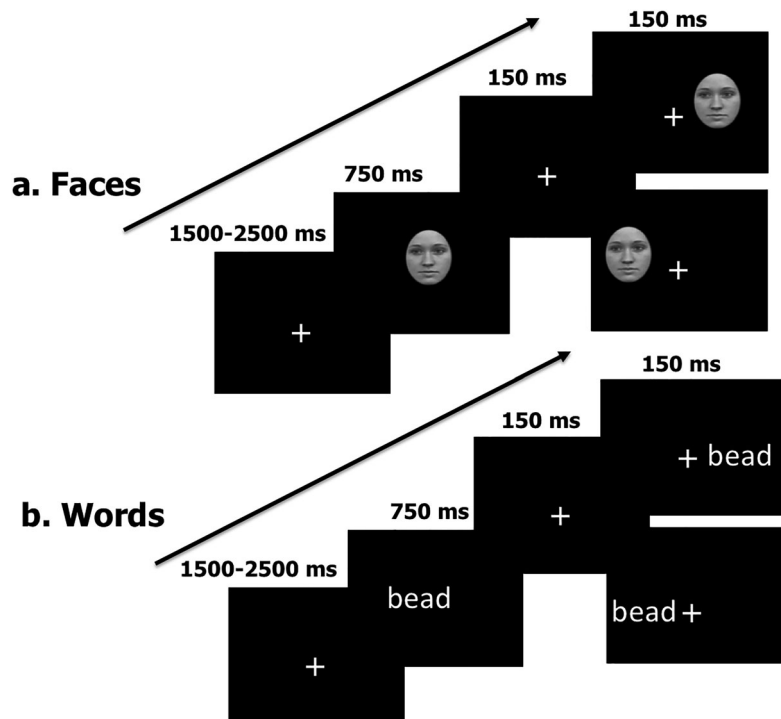
Stimuli

Sixty face images, half male, obtained from the Face-Place Database Project (Copyright 2008, Dr M. Tarr), were used (see examples in Figure 1). All faces were forward facing with a neutral expression. Faces were cropped to remove hair cues and presented in grey scale against a black background. Stimuli were 1.5 inches in height and 1 inch in width, yielding visual angles of 4.8 and 3.2 degrees respectively. On each trial, the pair of faces matched in gender.

Word stimuli consisted of 60 four-letter words (30 pairs), presented in grey, Arial, 18-point font against a black background (see examples in Figure 1). Stimuli were roughly 0.5 inches in height and 1 inch in width, yielding visual angles of 1.6 and 3.2 degrees, respectively. Pairs differed by one of the interior letters; half of the words differed in the second letter and half differed in the third.

Procedure

The experiment was run using E-prime software. Participants sat 24 inches from the display monitor. Face and word trials were randomly intermixed in a block and there were six blocks of trials (192 trials per block; total trials = 1152). On each trial, participants determined whether two sequentially presented stimuli were the same or not, and indicated their response by pressing two keys on a keyboard (responses counterbalances across participants) (see Figure 1 for depiction of trial sequence). Participants were instructed to perform as accurately as possible. Each trial consisted of a central fixation (jittered between 1500–2500 ms), which was followed by a centrally presented stimulus (750 ms). Immediately thereafter, a fixation appeared briefly (150 ms) and

**Figure 1.** Schematic depiction demonstrating the procedure for a single trial for faces (a) and words (b), respectively. Note both the central stimulus presentation followed by the lateralized probe stimulus.

then a second stimulus was presented in either the LVF or the RVF. The location of the second stimulus in the RVF or LVF was random but, across all trials, occurred with equal probability in the two fields. The centre of the lateralized stimulus was 5.3 degrees from fixation.

EEG recording

For roughly half the control (12/22) and all the atypical participants, electroencephalogram scalp recordings were acquired from 64 Ag/AgCl sintered electrodes embedded in a fibre Quik-Cap arranged according to the 10–20 naming system. Neuroscan 4 software was used to collect data on a Dell optiplex 360 computer. Both mastoid electrodes were placed on the participant, with the left serving as the online reference during recording. EEG signal was continuously recorded (1000 Hz sampling rate) and amplified with a band pass filter of 0.1–200 Hz.

For the remaining 10 control subjects, recordings were obtained using a 128-channel BioSemi Active Two system (BioSemi, Amsterdam, Netherlands), digitized at a 512-Hz rate with a 24-bit A/D conversion. All EEG data were preprocessed and analysed identically. Importantly, there was no difference between recording systems on the average amplitudes, taken across both stimulus conditions, of either the P100 ($t(20) = 0.62$; $p = .542$) or the N170 ($t(20) = 2.76$; $p = .78$) between our control participants, suggesting a similar signal-to-noise ratio in our dependent variables.

ERP preprocessing and analysis

EEG analysis was performed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) packages within MATLAB (Mathworks, Natick, MA).

The EEG recording was low pass filtered at a half-amplitude cut-off at 30 Hz, high pass filtered at 0.1 Hz, and re-referenced to the vertex (CZ) electrode. The filtered signal was divided into 1 second epochs (200 ms prestimulus to 800 ms post stimulus) and baseline corrected in the initial 200 ms prestimulus window. Individual epochs were excluded from the analysis if they contained eye blinks, or other artefacts in the -100 ms to 300 ms time window, using a sliding window peak-to-peak amplitude rejection algorithm.

ERPs were created for each participant by averaging all non-rejected epochs within each condition, yielding ERP waveforms for each participant. ERP peak amplitudes were derived for the P100 as the peak of the waveform between 75–150 ms and for the N170 waveform between 130–230 ms. Electrodes were selected for analysis based on previous literature showing lateral occipitotemporal sites exhibiting the largest N170 effects (e.g., Bentin et al., 2007; De Gelder & Stekelenburg, 2005; Towler, Gosling, Duchaine, & Eimer, 2012), and thus, we focused our analyses on the peak ERP amplitudes from electrodes P7 and P8.

Results

First, we summarize the behavioural findings from the half-field task, followed by the ERP analyses of the P100 and N170 waveforms elicited by faces and words presented centrally (as was done in Dundas et al., 2014). In each case, we summarize interactions at the group level using linear mixed models, before completing more in-depth analyses within each group using repeated measures ANOVAs to elucidate the nature of hemispheric preferences for words and faces. Within each group, we also made specific pairwise comparisons to test predictions laid out previously. To qualify the strength of evidence in these comparisons, we included both Cohen's d to reflect effect size and Bayes Factor (BF). BF was calculated for all pairwise comparisons (both behaviour and ERPs) using the "BayesFactor" package in R, with default priors. Each reported BF is the ratio of probability of the data given the alternative hypothesis over the probability of the data given the null hypothesis (Jeffreys, 1939). A BF less than 1 suggests support for the null hypothesis. A BF from 1–3 suggests anecdotal support for the alternative hypothesis and a BF greater than 3 suggests strong support for the alternative hypothesis (Wetzels et al., 2011).

Behaviour

Mean inverse efficiency (IE = reaction time/accuracy) for face and word matching for each of the three groups is summarized in Figure 2. We utilized inverse efficiency as our dependent measure to account for possible participant speed accuracy trade-offs, with lower IE scores denoting better

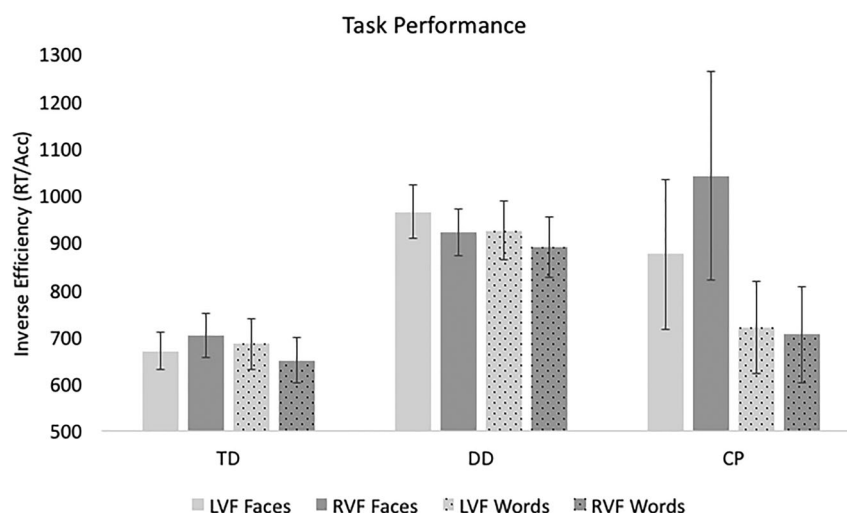


Figure 2. Mean inverse efficiency (RT/ACC) (and 1 SE) as a function of visual field presentation for faces and words in the healthy control (TD) group, the developmental dyslexic (DD) group, and the congenital prosopagnosia (CP) group.

performance (Townsend & Ashby, 1983). Inverse efficiency, therefore, captures performance of participants with diverging task strategies. A linear mixed effects model using stimulus (Face/Word) as the within-subjects factor and group (CP/TD/DD) as a between-subjects factor with the hemifield difference score (ensuring homogeneity of variance) on inverse efficiency as the dependent measure (Face IE = RVF IE – LVF IE; Word IE = LVF IE – RVF IE) yielded a significant stimulus \times group interaction ($F(2,36) = 5.70$; $p = .01$). There was no main effect of stimulus ($F(1,36) = 0.08$; $p = .78$). In a direct comparison against the TDs, the DD group performed more poorly with both faces ($t(30) = 4.63$; $p < .001$; $d = 1.71$) and words ($t(30) = 3.32$; $p = .002$; $d = 1.25$). In contrast, CPs performed more poorly on faces ($t(27) = 2.37$; $p = .02$; $d = 0.85$) compared to controls, but equally well with words ($t(27) = 0.51$; $p = .62$; $d = 0.20$). To elucidate the nature of the stimulus \times group interaction for hemifield difference scores, we completed within-subjects analyses at the level of individual hemifields.

Within the control (TD) group, a repeated measures ANOVA revealed a significant field \times stimulus interaction ($F(1,21) = 6.56$; $p = .01$; $\eta^2 = 0.24$), but no main effects of field ($F(1,21) = 0.003$; $p = .96$; $\eta^2 < 0.001$) or stimulus ($F(1,21) = 0.54$; $p = .46$; $\eta^2 = 0.02$). Given the significant interaction, we conducted pairwise tests in line with our a priori predictions. TDs performed better with words presented to the RVF, than the LVF ($t(21) = 2.21$; $p = .03$; $d = 0.51$, $BF = 1.6$), but no difference in performance for faces between hemifields ($t(21) = 1.57$; $p = .13$; $d = 0.35$, $BF = 0.644$).

In contrast to the TD group, the data from the DD group evinced no significant interaction of field and stimulus ($F(1,9) = 0.064$; $p = .806$; $\eta^2 = 0.007$), and no main effect stimulus ($F(1,9) = 1.08$; $p = .32$; $\eta^2 = 0.11$). There was a main effect of field ($F(1,9) = 5.45$; $p = .04$; $\eta^2 = 0.37$) indicating better performance in the RVF compared to the LVF. Similarly to the control group, DDs also performed better with words in the RVF than LVF ($t(9) = 2.41$; $p = .04$; $d = 0.77$, $BF = 2.11$). However, DDs performed equally well with faces between visual fields ($t(9) = 1.41$; $p = .19$, $BF = 0.671$), suggesting, perhaps, that single word discrimination is easier than discrimination of novel faces.

Finally, the CP group also showed a field \times stimulus interaction ($F(1,6) = 8.80$; $p = .03$; $\eta^2 = 0.60$), and a non-significant trending main effects of stimulus ($F(1,6) = 4.53$; $p = .07$; $\eta^2 = 0.43$), but no effect of visual field ($F(1,6) = 2.59$; $p = .16$; $\eta^2 = 0.30$). There was no difference in performance for words between visual fields ($t(6) = 0.41$; $p = .70$; $BF = 0.378$), but a second pairwise comparison revealed marginally better performance for faces in the LVF compared to the RVF ($t(6) = 2.36$; $p = .06$, $BF = 1.82$).

In sum, these findings demonstrate reliable deficits in both face and word processing for DDs, possibly speaking to the interdependent development of word and face processing. These differences exist despite the fact that the DD individuals are university students who, presumably, have acquired competent single word recognition skills and the task here might have been less challenging (unlike the clinical assessments) in eliciting a word recognition deficit.

The presence of a selective CP face processing deficit in the absence of a word processing deficit, in combination with the DD behavioural pattern, provides clear support for the directionality of face and word processing development interdependence.

Finally, these findings do and do not reveal some expected hemispheric differences. First, the TD data showed the expected RVF advantage for words but no LVF advantage for faces. Second, DDs showed a RVF advantage for words, but no advantage for faces. In contrast, there was an interaction of field and stimulus for CPs, and the LVF advantage for faces was also significant. These hemispheric preferences diverge from our predictions and may reflect the challenge in elucidating single hemispheric contributions to perceptual decisions. Certainly, both hemispheres contribute to the response in our task, but the degree to which each does so remains unclear. What remains to be determined is whether the electrophysiological measures uncover any group differences in hemispheric laterality for these two groups of stimuli.

ERP analysis

Analysis was completed on both the P100 and N170 components, as previous research has implicated alterations to these components in prosopagnosia (e.g., Eimer, Gosling, & Duchaine, 2012; Righart & de Gelder, 2007; Towler et al., 2012).

Figure 3 presents the grand average (mean across participants) ERPs at two lateral occipital electrodes, P7 and P8, for all three groups, elicited by the centrally presented stimuli. Qualitatively, the TD aggregate wave forms reveal the expected greater negative deflection for faces over the RH than LH and for words over the LH than RH within the predicted temporal interval, approximately 170 ms post stimulus-onset. To compare the electrophysiological profiles of the other two groups against the TD group, the relevant components of the waveform were quantified. Figures 4 and 5 show the peak amplitudes (in microvolts) for the P100 and N170 components elicited by faces and words, respectively.

Prior to comparing between different conditions within and between groups, we compared the global amplitude between groups across all conditions containing centrally presented stimuli. We calculated subject level peak P100 and N170 amplitudes by averaging over all presentation conditions for each subject at both P7 and P8 electrodes from 75–150 ms and 130–230 ms respectively, and then compared the three groups at each ERP component. We found no difference in global amplitude in one way ANOVAs with respect to either the P100, $F(2,38) = 0.64$; $p = .53$, or the N170, $F(2,38) = 0.05$; $p = .94$, components. Thus, any differences in hemispheric organization cannot be simply explained by group differences in overall signal strength.

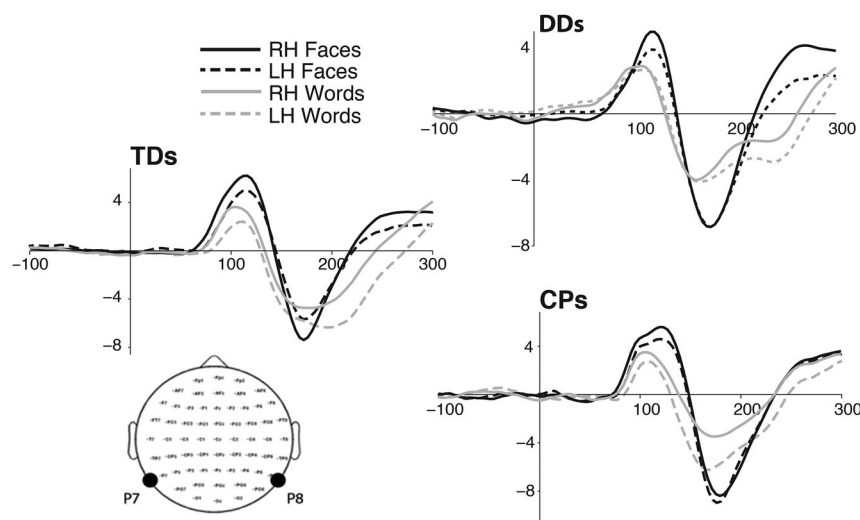


Figure 3. Group averaged ERP waveforms (–100 ms to 300 ms) measured from the P7 (LH) and P8 (RH) electrodes in both typically developed (TD) controls, developmental dyslexic (DD), and congenital prosopagnosia (CP) groups elicited by centrally presented faces and words.

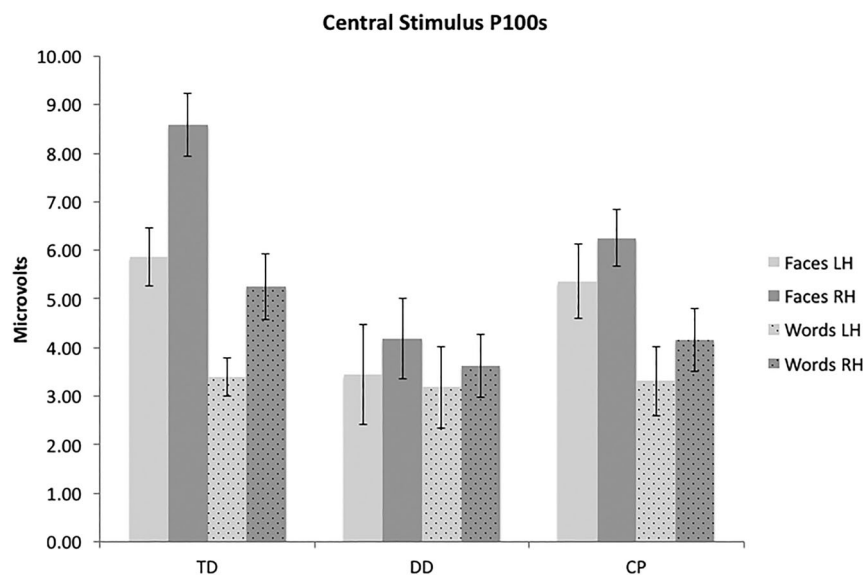


Figure 4. Peak amplitude (and 1 SE) of P100 waveforms elicited by centrally presented stimuli in the healthy control (TD), developmental dyslexic (DD), and prosopagnosia (CP) groups. Amplitudes are shown for both left (P7) and right (P8) hemisphere electrodes.

In the P100 analysis, a linear mixed effects model, with stimulus type and hemisphere as within-subjects factors and group as the between-subjects factor, did not reveal a significant three-way interaction of stimulus \times group \times hemisphere ($F(2,108) = 0.83$; $p = .44$), or a two way interaction of stimulus \times group ($F(2,108) = 1.22$; $p = .30$). However, there were interactions of stimulus \times hemisphere ($F(1,108) = 6.92$; $p = .01$), and hemisphere \times group ($F(2,108) = 7.58$; $p < .001$), and main effects of stimulus ($F(1,108) = 53.5$; $p < .001$), with faces eliciting larger P100s than words, and of hemisphere (Figure 4), ($F(1,108) = 97.7$; $p < .001$), with

larger P100s in the RH than the LH. Because there was no significant or trending three-way interaction, we did not pursue this analysis any further.

In the analysis of the N170 component (see Figure 5; note, for ease of viewing, negative is plotted upward on the y-axis), a linear mixed effects model revealed a non-significant, but clearly trending stimulus \times hemisphere \times group interaction ($F(2,108) = 2.51$; $p = .08$) and hemisphere \times group interaction ($F(2,108) = 2.79$; $p = .07$). There was a significant stimulus \times hemisphere interaction ($F(1,108) = 28.2$; $p < .001$) and main effects of stimulus type ($F(1,108) = 17.5$;

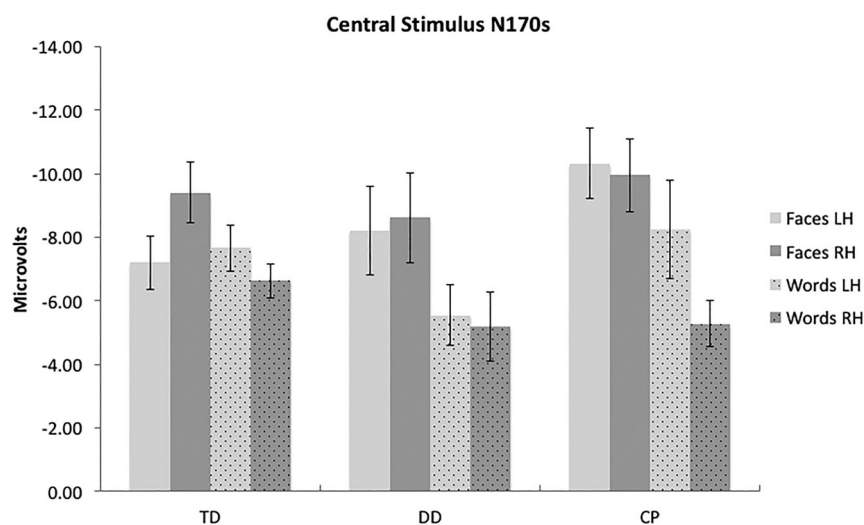


Figure 5. Peak amplitude (and 1 SE) of N170 waveforms elicited by centrally presented stimuli in the healthy control (TD), developmental dyslexic (DD), and prosopagnosia (CP) groups. Amplitudes are shown for both left (P7) and right (P8) hemisphere electrodes.

$p < .001$), with faces eliciting larger N170s than words, and hemisphere ($F(1,108) = 8.78$; $p = .004$), with the RH evincing larger responses. The stimulus \times group interaction ($F(2,108) = 2.29$; $p = .10$) was not significant. Given the marginally significant three-way interaction and our specific a priori predictions with respect to differential hemispheric organization for the two stimulus types in the three groups, we completed analyses within each group alone.

In the TD group, a repeated measures ANOVA revealed a significant stimulus \times hemisphere interaction ($F(1,21) = 13.6$; $p = .001$; $\eta^2 = 0.39$), but no main effects of stimulus ($F(1,21) = 1.63$; $p = .22$; $\eta^2 = 0.07$), or hemisphere ($F(1,21) = 0.66$; $p = .42$; $\eta^2 = 0.03$). Pairwise tests revealed that faces elicited a larger N170 in the RH compared to the LH ($t(21) = 2.71$; $p = .01$; $d = 0.58$, $BF = 3.95$), and words elicited a larger N170 in the LH compared to the RH ($t(21) = 2.24$; $p = .03$; $d = 0.51$, $BF = 1.73$).

In the DD group, the same repeated measures ANOVA revealed no significant stimulus \times hemisphere interaction ($F(1,9) = 0.27$; $p = .61$; $\eta^2 = 0.02$), and no main effect of hemisphere ($F(1,9) = 0.17$; $p = .68$; $\eta^2 = 0.01$). There was a main effect of stimulus ($F(1,9) = 5.95$; $p = .03$; $\eta^2 = 0.40$), demonstrating larger N170s for faces compared to words. However, there was no observable pattern of laterality whatsoever for DDs. Faces elicited equally large N170s in LH and RH ($t(9) = 0.53$; $p = .61$, $BF = 0.34$). Words also failed to elicit any reliable difference in N170 peaks between hemispheres ($t(9) = 0.39$; $p = .70$, $BF = 0.32$). Note for that both pairwise comparisons, BF shows evidence in favour of the null hypothesis.

Finally, the same analysis used above but now with the data from the CPs revealed a significant stimulus \times hemisphere interaction ($F(1,6) = 7.42$; $p = .03$; $\eta^2 = 0.55$), but no main effects of stimulus ($F(1,6) = 3.11$; $p = .13$; $\eta^2 = 0.34$), or hemisphere ($F(1,6) = 1.84$; $p = .22$; $\eta^2 = 0.23$). Pairwise comparisons between hemispheres for each stimulus type showed that CPs produced non-significant trend with larger word N170s in the LH compared to the RH ($t(6) = 2.03$; $p = .08$; $d = 0.91$, $BF = 1.73$), but showed no differences between hemispheres for face N170s ($t(6) = 0.24$; $p = .81$, $BF = 0.362$). The non-significant word advantage in the LH, together with anecdotal evidence for the alternative hypothesis from the BF analysis, and a large effect size might suggest a true effect in the context of an underpowered sample in the CP group.

Taken together, the electrophysiological evidence presented here provides clear evidence that TD individuals exhibit the expected left and RH laterality patterns for words and faces, respectively. In sharp contrast, DDs failed to show any pattern of hemispheric specialization for any stimulus type. That is, they produced neither the right hemispheric preference for faces, nor the LH preference for words. BF confirmed support for the null hypotheses in both word and face contrasts. On the other hand, CPs showed a non-significant trend for normal word lateralization in the LH, but did not show any hemispheric lateralization pattern for faces. BF confirmed evidence for the null hypothesis in lateralization for faces only. Furthermore, the between-group difference in lateralization patterns was unique to the N170 and did not extend to the earlier P100 ERP component, and could not be explained by difference in overall signal amplitude.

Discussion

The goal of the current study was twofold: to explore further the interdependent development of face and word processing, and to evaluate the impact of atypical development in one domain on a second domain, here face recognition on word recognition (and vice versa). We sought to test predictions made by a theoretical account and associated empirical data (Behrmann & Plaut, 2015; Dundas, Plaut, & Behrmann, 2013, 2014; Plaut & Behrmann, 2011) which argues for the interdependence of the development of hemispheric organization for words with that of faces. Specifically, the claim is that, during the course of acquiring word recognition skills, the pressure to couple visual orthographic and language representations in the LH results in competition with the representation of faces. As a result of this competition, these face representations become largely (albeit not exclusively) lateralized in the RH. Furthermore, this account predicts that if the lateralization of words emerges prior to the lateralization of faces, then the atypical acquisition of word recognition should give rise to altered lateralization for words and should also adversely impact the lateralization of faces. Given the proposed chronology of acquisition, the account also predicts that the atypical acquisition of face recognition should give rise to

altered lateralization for faces but that this should have no impact on the (prior) lateralization of words.

By comparing individuals with DD to a control group, we tested the first hypothesis that atypical word reading disrupts both word and face processing. Only when we consider the second set of comparisons of the group of individuals with CP and controls can we test the directionality of the predictions made by the theory. That is, the disruption of typical face processing in the presence of normal word processing provide support for a specific directionality in the interdependent account of perceptual development.

To test these predictions and the key asymmetry between them, we recorded behavioural inverse efficiency and ERPs from adults with DD and from adults with CP. We contrasted the lateralization profiles of the two groups and also compared them with the profile of normal controls in a hemifield presentation paradigm in response to word and face stimuli. We found that, relative to TDs, individuals with DD exhibited reliable face and word processing deficits. CPs also exhibited face processing deficits relative to TDs, but no deficit in word processing.

In the analysis of the N170 component elicited by words and faces presented centrally, controls evinced the typical hemispheric organization for both categories, showing larger word N170s in the LH than RH and larger face N170s in the RH than LH. In contrast, the DDs did not evince either of the typical patterns in hemispheric organization for words and faces. Furthermore, the CPs evinced the typical hemispheric organization only for words (though marginally), but not for faces. By comparing global amplitude of P100s and N170s across groups, we showed that the failure to find typical laterality patterns in DDs and CPs was not a result of differences in overall ERP amplitude between groups. This difference in hemispheric organization across the three groups was unique to the N170, as no group differences were found in the P100.

Before considering the findings in light of the predictions derived from the theory, we briefly argue that null findings in the form of no laterality patterns in ERP data for DDs does not reflect an underpowered sample. First, the CPs evinced a normal pattern of N170 lateralization for words, as well as a significant hemisphere \times stimulus interaction, with even fewer subjects than the DD group. Secondly, the DD group

did show a significant visual field preference behaviourally, suggesting that differences within the DD group are detectable with only 10 subjects. Third, calculation of BF shows evidence in support of the null hypothesis for both word and face ERP lateralization, in contrast to the comparisons in both the TD and CP groups. Finally, there were no overall amplitude differences between any of the groups, which demonstrates that DDs do not evince a smaller magnitude ERP signal. Together, the null findings for the DD group provide clear evidence that DDs show no hemispheric differences in peak N170 amplitude for either words or faces.

The theory by Behrmann and Plaut (2015) and Plaut and Behrmann (2011) predicts a specific direction in the relationship between face and word processing. That is, during development, the competition between words and faces in the LH pushes the representation for faces towards lateralization in the RH, but that the development of face processing does not affect the hemispheric organization for words in the same manner. Additionally, this explanation makes the claim that the typical adult pattern for words emerges before that of faces. The prediction that follows suggests that the typical adult pattern found for words can develop in the absence of the typical development of face processing, but not vice versa. The results presented here clearly support the directionality proposed by this theory. Adult CPs did not show the typical hemispheric organization for faces; here, they showed no hemispheric preference at all for faces as measured by the N170. However, of great interest, adult CPs still evinced the typical word preference in the LH.

Evidence shows that distributed networks, rather than single regions may mediate processes in visual cognition (Behrmann & Plaut, 2013). Almost certainly, distributed neural networks mediate both visual word and face processing (Harris et al., 2016; Robinson, Plaut, & Behrmann, 2017). The degree to which nodes and connections in these networks overlap is not clear. Given the nature of high acuity visual processing, face and word networks likely overlap in their utilization of certain nodes in visual cortex (for example, the region of extrastriate cortex that represents the anterior extrapolation of the fovea; Levy et al., 2001). However, the underlying representations and associated semantics differ greatly between words and faces. This may manifest as non-overlapping network nodes at higher

levels of processing, perhaps at the level of the anterior temporal lobes. The network instantiation of the theory described above may simply be the changing of weights between non-shared and shared nodes over the course of development. The computational approach by Plaut and Behrmann (2011) provides the proof of principle. Furthermore, a network approach can inform the degree to which developmental disorders are selective for specific domains (Rosenthal et al., 2017).

Selectivity in developmental dyslexia

The behavioural results from DDs also shed light on the relative selectivity of the disorder. Traditionally thought to be selective to language representation, these findings suggest that the deficit also exists at the level of visual processing. In addition to the expected word processing deficit, we found that DDs were significantly worse in their performance with faces relative to controls. This further supports the account of graded, but overlapping asymmetry of word and face processing development. These findings also map nicely to atypical BOLD activity in both VWFA and FFA in DD (Monzalvo et al., 2012).

Conclusion

Using a hemifield presentation paradigm with words and faces as stimuli, we measured the P100 and N170 ERP components generated by adult DDs, CPs, and TD controls. Controls showed the standard RH preference for faces and LH preference for words as measured by the N170. DDs, however, showed no hemispheric preference for faces or words whatsoever. Lastly, CPs showed normal hemispheric organization for words, but not for faces. These findings support a theoretical account in which the development of word processing can occur normally in the absence of typically developing face processing, but not vice versa.

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References

- Avidan, G., & Behrmann, M. (2008). Implicit familiarity processing in congenital prosopagnosia. *Journal of Neuropsychology*, 2(1), 141–164.
- Avidan, G., Hasson, U., Malach, R., & Behrmann, M. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 2. Functional neuroimaging findings. *Journal of Cognitive Neuroscience*, 17(7), 1150–1167. doi:10.1162/0898929054475154
- Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences*, 104(21), 9087–9092.
- Behrmann, M., Avidan, G., Marotta, J. J., & Kimchi, R. (2005). Detailed exploration of face-related processing in congenital prosopagnosia: 1. Behavioral findings. *Journal of Cognitive Neuroscience*, 17(7), 1130–1149.
- Behrmann, M., & Plaut, D. C. (2013). Distributed circuits, not circumscribed centers, mediate visual recognition. *Trends in Cognitive Sciences*, 17(5), 210–219. doi:10.1016/j.tics.2013.03.007
- Behrmann, M., & Plaut, D. C. (2014). Bilateral hemispheric processing of words and faces: Evidence from word impairments in prosopagnosia and face impairments in pure alexia. *Cerebral Cortex*, 24(4), 1102–1118. doi:10.1093/cercor/bhs390
- Behrmann, M., & Plaut, D. C. (2015). A vision of graded hemispheric specialization. *Annals of the New York Academy of Sciences*, 1359(1), 30–46.
- Bentin, S., Degutis, J. M., D'Esposito, M., & Robertson, L. C. (2007). Too many trees to see the forest: Performance, event-related potential, and functional magnetic resonance imaging manifestations of integrative congenital prosopagnosia. *Journal of Cognitive Neuroscience*, 19(1), 132–146. doi:10.1162/jocn.2007.19.1.132
- Bishop, D. V. (2013). Cerebral asymmetry and language development: Cause, correlate, or consequence? *Science*, 340(6138), 1230531–1230531-8. doi:10.1126/science.1230531
- Brem, S., Bach, S., Kucian, K., Guttorm, T. K., Martin, E., Lyytinen, H., ... Richardson, U. (2010). Brain sensitivity to print emerges when children learn letter-speech sound correspondences. *Proceedings of the National Academy of Sciences*, 107(17), 7939–7944. doi:10.1073/pnas.0904402107
- Burns, E. J., Bennetts, R. J., Bate, S., Wright, V. C., Weidemann, C. T., & Tree, J. J. (2017). Intact word processing in

- developmental prosopagnosia. *Scientific Reports*, 7(1), 1–12. doi:10.1038/s41598-017-01917-8
- Cantlon, J. F., Pined, P., Dehaene, S., & Pelphrey, K. A. (2011). Cortical representations of symbols, objects, and faces are pruned back during early childhood. *Cerebral Cortex*, 21, 191–199.
- Dalrymple, K. a., Garrido, L., & Duchaine, B. (2014). Dissociation between face perception and face memory in adults, but not children, with developmental prosopagnosia. *Developmental Cognitive Neuroscience*, 10, 10–20. doi:10.1016/j.dcn.2014.07.003
- De Gelder, B., & Stekelenburg, J. J. (2005). Naso-temporal asymmetry of the N170 for processing faces in normal viewers but not in developmental prosopagnosia. *Neuroscience Letters*, 376(1), 40–45. doi:10.1016/j.neulet.2004.11.047
- Dehaene, S., Cohen, L., Morais, J., & Kolinsky, R. (2015). Illiterate to literate: Behavioral and cerebral changes induced by reading acquisition. *Nature Reviews Neuroscience*, 16, 234–244.
- Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21.
- Duchaine, B. C., Parker, H., & Nakayama, K. (2003). Normal recognition of emotion in a prosopagnosic. *Perception*, 32(7), 827–838.
- Duchaine, B., & Nakayama, K. (2006). The Cambridge Face Memory Test: Results for neurologically intact individuals and an investigation of its validity using inverted face stimuli and prosopagnosic participants. *Neuropsychologia*, 44(4), 576–585.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2012). The joint development of hemispheric lateralization for words and faces. *Journal of Vision*, 12(9), 22–22.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2013). The joint development of hemispheric lateralization for words and faces. *Journal of Experimental Psychology: General*, 142(2), 348–358.
- Dundas, E. M., Plaut, D. C., & Behrmann, M. (2014). An ERP investigation of the co-development of hemispheric lateralization of face and word recognition. *Neuropsychologia*, 61, 315–323.
- Eimer, M., Gosling, A., & Duchaine, B. (2012). Electrophysiological markers of covert face recognition in developmental prosopagnosia. *Brain*, 135(2), 542–554. doi:10.1093/brain/awr347
- Farah, M. J., Rabinowitz, C., Quinn, G. E., & Liu, G. T. (2000). Early commitment of neural substrates for face recognition. *Cognitive Neuropsychology*, 17(1–3), 117–123.
- Gabay, Y., Dundas, E., Plaut, D. C., & Behrmann, M. (2017). Atypical perceptual processing of faces in developmental dyslexia. *Brain and Language*, 173, 41–51.
- Garrido, L., Duchaine, B., & Nakayama, K. (2008). Face detection in normal and prosopagnosic individuals. *Journal of Neuropsychology*, 2(1), 119–140.
- Geskin, J., & Behrmann, M. (2017). Congenital prosopagnosia without object agnosia: A literature review. *Cognitive Neuropsychology*, in press with commentaries.
- Harris, R. J., Rice, G. E., Young, A. W., & Andrews, T. J. (2016). Distinct but overlapping patterns of response to words and faces in the fusiform gyrus. *Cerebral Cortex*, 26(7), 3161–3168. doi:10.1093/cercor/bhv147
- Hasson, U., Harel, M., Levy, I., & Malach, R. (2003). Large-scale mirror-symmetry organization of human occipito-temporal object areas. *Neuron*, 37(6), 1027–1041.
- Hasson, U., Levy, I., Behrmann, M., Hendler, T., & Malach, R. (2002). Center-biased representation for characters in the human ventral visual stream. *Neuron*, 34, 479–490.
- Humphreys, K., Avidan, G., & Behrmann, M. (2007). A detailed investigation of facial expression processing in congenital prosopagnosia as compared to acquired prosopagnosia. *Experimental Brain Research*, 176(2), 356–373.
- Jeffreys, H. (1939). *Theory of probability*. New York, NY: Oxford University Press.
- Klingberg, T., Hedehus, M., Temple, E., Salz, T., Gabrieli, J. D., Moseley, M. E., & Poldrack, R. A. (2000). Microstructure of temporo-parietal white matter as a basis for reading ability: Evidence from diffusion tensor magnetic resonance imaging. *Neuron*, 25(2), 493–500. doi:10.1016/S0924-9338(02)80215-2
- Langer, N., Benjamin, C., Minas, J., & Gaab, N. (2013). The neural correlates of reading fluency deficits in children. *Cerebral Cortex*, 25(6), 1441–1453.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center-periphery organization of human object areas. *Nature Neuroscience*, 4(5), 533–539.
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: An open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8, 213. doi:10.3389/fnhum.2014.00213
- Maisog, J. M., Einbinder, E. R., Flowers, D. L., Turkeltaub, P. E., & Eden, G. F. (2008). A meta-analysis of functional neuroimaging studies of dyslexia. *Annals of the New York Academy of Sciences*, 1145(1), 237–259.
- Maurer, U., Brem, S., Kranz, F., Bucher, K., Benz, R., Halder, P., ... Brandeis, D. (2006). Coarse neural tuning for print peaks when children learn to read. *Neuroimage*, 33, 749–758. doi:10.1016/j.neuroimage.2006.06.025
- Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., & Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socioeconomic status. *Neuroimage*, 61, 258–274.
- Nunn, J. A., Postma, P., & Pearson, R. (2001). Developmental prosopagnosia: Should it be taken at face value? *Neurocase*, 7(1), 15–27.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9(1), 97–113.
- Plaut, D. C., & Behrmann, M. (2011). Complementary neural representations for faces and words: A computational exploration. *Cognitive Neuropsychology*, 28(3–4), 251–275.
- Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., ... Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews*, 6(3), 207–213.

- Richlan, F., Kronbichler, M., & Wimmer, H. (2013). Structural abnormalities in the dyslexic brain: A meta-analysis of voxel-based morphometry studies. *Human Brain Mapping*, 34(11), 3055–3065. doi:10.1002/hbm.22127
- Righart, R., & de Gelder, B. (2007). Impaired face and body perception in developmental prosopagnosia. *Proceedings of the National Academy of Sciences of the United States of America*, 104(43), 17234–17238. doi:10.1073/pnas.0707753104
- Roberts, D. J., Lambon Ralph, M. A., Kim, E., Tainturier, M. J., Beeson, P. M., Rapcsak, S. Z., & Woollams, A. M. (2015). Processing deficits for familiar and novel faces in patients with left posterior fusiform lesions. *Cortex*, 72, 79–96.
- Robinson, A. K., Plaut, D. C., & Behrmann, M. (2017). Word and face processing engage overlapping distributed networks: Evidence from RSVP and EEG investigations. *Journal of Experimental Psychology-General*, 146(7), 943–961. doi:10.1037/xge0000302
- Rosenthal, G., Tanzer, M., Simony, E., Hasson, U., Behrmann, M., & Avidan, G. (2017). Altered topology of neural circuits in congenital prosopagnosia. *eLife*, 6, e25069. doi:10.7554/eLife.25069
- Rubino, C., Corrow, S. L., Corrow, J. C., Duchaine, B., & Barton, J. J. (2016). Word and text processing in developmental prosopagnosia. *Cognitive Neuropsychology*, 33(5–6), 315–328.
- Salmelin, R., Kiesilä, P., Uutela, K., Service, E., & Salonen, O. (1996). Impaired visual word processing in dyslexia revealed with magnetoencephalography. *Annals of Neurology*, 40(2), 157–162.
- Schmalzl, L., Palermo, R., Harris, I. M., & Coltheart, M. (2009). Face inversion superiority in a case of prosopagnosia following congenital brain abnormalities: What can it tell us about the specificity and origin of face-processing mechanisms? *Cognitive Neuropsychology*, 26(3), 286–306. doi:10.1080/02643290903086904
- Sigurdardottir, H. M., Ívarsson, E., Kristinsdóttir, K., & Kristjánsson, Á. (2015). Impaired recognition of faces and objects in dyslexia: Evidence for ventral stream dysfunction? *Neuropsychology*, 29(5), 739–750.
- Starrfelt, R., Klargaard, S. K., Petersen, A., & Gerlach, C. (2017). Are reading and face processing related? An investigation of reading in developmental prosopagnosia. *Neuropsychologia*, in press. doi:10.1101/039065
- Thomas, C., Avidan, G., Humphreys, K., Jung, K. J., Gao, F., & Behrmann, M. (2009). Reduced structural connectivity in ventral visual cortex in congenital prosopagnosia. *Nature Neuroscience*, 12(1), 29–31. doi:10.1038/nn.2224
- Torgesen, J. K., Wagner, R., & Rashotte, C. (1999). *TOWRE–2 test of word reading efficiency*. Austin, TX: Pro-Ed.
- Towler, J., Gosling, A., Duchaine, B., & Eimer, M. (2012). The face-sensitive N170 component in developmental prosopagnosia. *Neuropsychologia*, 50(14), 3588–3599. doi:10.1016/j.neuropsychologia.2012.10.017
- Townsend, J. T., & Ashby, F. G. (1983). *Stochastic modeling of elementary psychological processes*. New York, NY: Cambridge University Press.
- Wandell, B. A., Rauschecker, A. M., & Yeatman, J. D. (2012). Learning to see words. *Annual Review of Psychology*, 63, 31–53.
- Wetzels, R., Matzke, D., Lee, M. D., Rouder, J. N., Iverson, G. J., & Wagenmakers, E. J. (2011). Statistical evidence in experimental psychology: An empirical comparison using 855 t tests. *Perspectives on Psychological Science*, 6(3), 291–298.
- Woodhead, Z. V., Wise, R. J., Sereno, M., & Leech, R. (2011). Dissociation of sensitivity to spatial frequency in word and face preferential areas of the fusiform gyrus. *Cerebral Cortex*, 21(10), 2307–2312.