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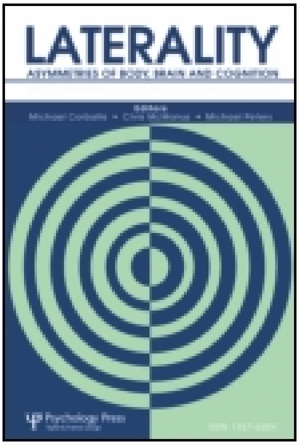

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Individual differences in reading skill and language lateralisation: A cluster analysis

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Individual differences in reading and cerebral lateralisation were investigated in 200 college students who completed reading assessments and divided visual field word recognition tasks, and received a structural MRI scan. Prior studies on this data set indicated that little variance in brain–behaviour correlations could be attributed to the effects of sex and handedness variables (Chiarello, Welcome, Halderman, & Leonard, 2009; Chiarello, Welcome, Halderman, Towler, et al., 2009; Welcome et al., 2009). Here a more bottom-up approach to behavioural classification (cluster analysis) was used to explore individual differences that need not depend on a priori decisions about relevant subgroups. The cluster solution identified four subgroups of college age readers with differing reading skill and visual field lateralisation profiles. These findings generalised to measures that were not included in the cluster analysis. Poorer reading skill was associated with somewhat reduced VF asymmetry, while average readers demonstrated exaggerated RVF/left hemisphere advantages. Skilled readers had either reduced asymmetries, or asymmetries that varied by task. The clusters did not differ by sex or handedness, suggesting that there are identifiable sources of variance among individuals that are not captured by these standard participant variables. All clusters had typical leftward asymmetry of the planum temporale. However, the size of areas in the posterior corpus callosum distinguished the two subgroups with high reading skill. A total of 17 participants, identified as multivariate outliers, had unusual behavioural profiles and differed from the remainder of the sample in not having significant leftward asymmetry of the planum temporale. A less buffered type of neurodevelopment that is more open to the effects of random genetic and environmental influences may characterise such individuals.

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It is widely acknowledged that individual differences moderate brain–behaviour relationships (e.g., Colcombe, Kramer, Erickson, & Scalf, 2005; Ganis, Thompson, & Kosslyn, 2005). Left hemisphere language specialisation, for example, varies in degree across individuals, and some persons demonstrate little asymmetry or reversed asymmetry, whether this is measured behaviourally, functionally, or anatomically (Chiarello, Welcome, Halderman, Towler, et al., 2009; Kaiser, Kuenzli, Zappatore, & Nitsch, 2007; Prat, Long, & Baynes, 2007). There are both theoretical and applied reasons for investigating individual differences in brain organisation. Theoretically, an emphasis on variation is essential in order to place psychological phenomena within a biological framework, where variability is of central interest rather than being treated as unfortunate "noise" (Kosslyn et al., 2002). In applied settings clinicians draw on our science to evaluate and treat individuals (Cherney & Small, 2006), yet they must frequently rely on knowledge of group averages to inform treatment strategies without a full appreciation of the range of normal (premorbid) structure–function associations.

With respect to reading, a highly skilled behaviour that is unevenly developed in the population, research has emphasised comparisons between dyslexic and typical readers (e.g., Leonard & Eckert, 2008). However, the typical reading controls in such studies are usually treated as an undifferentiated group and provide little information about the relationships between variations in reading skill and lateralisation within the normal reading population. In the current study we explore a multivariate approach (cluster analysis) to investigate whether differing behavioural/lateralisation profiles can be observed among typical college age readers.

Prior neuropsychological studies of individual differences have employed one of two methods. Some insight can be derived from regression approaches, in which one examines whether the magnitude of a neural variable predicts the degree of a behavioural variation. For example, Forstman et al. (2008) reported that activation of the right inferior frontal cortex correlated with a reaction time measure of response inhibition. In some cases multiple regression techniques can be used to determine the influence of additional variables on brain–behaviour relationships and/or to hold constant potentially confounding variables (e.g., Peterson, Gable, & Harmon-Jones, 2007). This approach can capture broad patterns across the studied population, but leaves open the question of whether there may be meaningful subpopulations with different structure/function relationships.

For example, if one observes a .4 correlation, are the individuals with scores near the regression line different in important ways from those with scores that are more distant from this line? Perhaps the latter individuals have behaviour that is predicted by a different set of neurofunctional variables. This idea is difficult to assess directly within a regression framework.

An alternative approach is to identify groups a priori and then investigate whether these groups differ in behavioural or neuropsychological variables. The voluminous neuropsychological literature on differences attributable to sex, handedness, or diagnostic category attests to the popularity of this approach (e.g., Harrington & Tomaszewski, 2008; Narr et al., 2007; Sommer, Aleman, Bouma, & Kahn, 2004; Sommer, Aleman, Somers, Boks, & Kahn, 2008; Wallentin, 2009). This method has the advantage that groups can be objectively and reliably determined, and it addresses the natural curiosity about potential neural differences among individuals who can be readily distinguished from each other. We have previously employed this approach to investigate sex differences (Chiarello, Welcome, Halderman, Towler, et al., 2009; Leonard, Towler, Welcome, & Chiarello, 2009; Leonard et al., 2008), handedness differences (Chiarello, Welcome, Halderman, & Leonard, 2009), and sex/handedness groups (Welcome et al., 2009) in the sample reported here. However, very little variance in brain structure and behaviour was explained by these variables. No sex differences in corpus callosum area or in the volumes of language-relevant cortex were obtained after controlling for brain volume (Leonard et al., 2008; Welcome et al., 2009), nor were there sex differences in perisylvian asymmetries (Chiarello, Welcome, Halderman, Towler, et al., 2009). With respect to behavioural (divided visual field) asymmetries, very small sex differences (accounting for 2% of the total variance) were observed in only two of eight lexical tasks, and these could not be replicated in independent subsamples (Chiarello, Welcome, Halderman, Towler, et al., 2009). Similarly there were no significant differences between consistent handers (those with strong hand preference for five of five activities) and mixed handers[1] in VF asymmetry (Chiarello, Welcome, Halderman, & Leonard, 2009), corpus callosum area (Welcome et al., 2009), or perisylvian asymmetries (unpublished data). Hence the current investigation was motivated by the realisation that most of the individual variation in

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[1] Participant recruitment for this project was unrestricted for handedness so as to obtain a representative sample of the college age population. Hence there are a relatively small number of left handers ($N = 22$, 11% of sample), precluding strong statistical comparisons between left- and right-handers. For this reason we have explored differences between mixed- ($N = 97$) and consistent-handers ($N = 103$) within our sample. There is an increasing amount of evidence for a variety of behavioural differences between these groups (e.g., Christman, Varalakshmi, & Jasper, 2009; Propper, Christman, & Phaneuf, 2005).

reading skill, and in cerebral asymmetry, was not captured by categorising people into sex or handedness groups.

Some investigations have gone beyond these ubiquitous grouping variables to explore differences related to particular individual traits. For example, Golestani, Molko, Dehaene, LeBihan, and Pallier (2007) found that fast learners of non-native speech sounds ($N = 11$) had greater white matter density in left Heschl's gyrus relative to slow learners ($N = 10$). Such studies can yield important insights, but must rely on the investigators' a priori ideas to identify participant characteristics that may most meaningfully reveal individual differences in brain function. Because individuals differ from each other along multiple dimensions, forming groups based on a single trait can only reveal a fraction of the diversity in the population.

Data gathered via the Biological Substrates for Language Project enabled us to explore an alternate approach to understanding individual differences. This approach (cluster analysis) makes no a priori assumptions about the relevant dimensions along which individuals might differ, in contrast to typical neuropsychological analyses of individual differences. The project collected demographic and reading test data, and divided visual field (VF) asymmetries for a variety of lexical tasks from 200 college students who also received a structural MRI scan. One goal of the project is to document the range of anatomical and behavioural asymmetries from a population of normal readers, and to begin to explore the relationship between neuroanatomical and behavioural variation. In the current investigation we made no assumptions about the relevant dimensions along which individuals might differ behaviourally. Instead we employed a statistical technique (cluster analysis) that groups similar individuals together based on their scores on multiple variables. This bottom-up approach is exploratory rather than confirmatory, in that it allows groups to emerge from the patterns inherent in the dataset rather than testing whether the data conform to groups determined a priori.

After clusters were identified from the reading and visual field scores we examined whether the groups so formed differed in neuroanatomical regions that may support lateralised functioning (planum temporale asymmetry and corpus callosum area). Leftward asymmetry of the planum temporale is quite robust, and encompasses posterior language-relevant cortex (Shapleske, Rossell, Woodruff, & David, 1999), and visual field asymmetries may vary with corpus callosum structure (e.g., Hellige, Taylor, Lesmes, & Peterson, 1998; Zaidel & Iacaboni, 2003). The current study was designed to explore the following questions:

1. Are there subgroups within the college population characterised by differing profiles of reading and VF/hemisphere asymmetry? If so, to what extent do these groups differ in standard demographic variables

such as sex and handedness? The answers to these questions can shed light on the relationship between reading skill and degree of visual lateralisation.

2. Do the groups identified by the cluster analysis differ in either planum temporale asymmetry or corpus callosum area? If so, this could suggest relationships between behavioural and neuroanatomical profiles that might not be transparent from alternate approaches that rely on sample-wide correlations or a priori participant groupings.
3. Are there some individuals whose reading behaviour and VF asymmetry depart from typically observed outcomes? In the current study these would be persons who showed the greatest multivariate deviation from the sample dataset (i.e., outliers). Do such individuals show unusual neuroanatomical features? We have suggested previously that some individuals may have less typical or well-regulated trajectories of neural development that can result in unusual neuroanatomical and behavioural asymmetries (Chiarello, Kacinik, Manowitz, Otto, & Leonard, 2004). Hence we would predict a higher likelihood of unusual neuroanatomical features in the MRI scans obtained from those identified behaviourally as multivariate outliers.

METHOD

Participants took part in five sessions of behavioural testing, and then received a structural MRI scan in their final session. Behavioural testing and preliminary analyses of these data were conducted at the University of California, Riverside, with the experimenters blind to the status of the brain measurements. Similarly, brain measurements were made at the University of Florida by anatomists who were blind to the identity and behavioural findings of the participants. The behavioural and anatomical data were pooled only after the data were scored and brain measurements completed.

Participants

Campus-wide electronic messages and announcements were used to recruit potential participants. In order to obtain a representative sample we did not attempt to recruit equal numbers of left- and right-handers. The study was approved by Institutional Review Boards at both the University of California and the University of Florida. A total of 100 male and 100 female university student volunteers participated, receiving $100 payment for their participation. Participants with a history of brain injury or disease, or conditions incompatible with an MRI scan, were excluded. A neuroradiologist reviewed all scans for pathology, and four additional participants were excluded from the final sample due to abnormal findings on the MRI.

All participants were native speakers of English with normal or corrected-to-normal vision. To assess handedness, a five-item preference questionnaire was utilised (Bryden, 1982), which yields an index ranging from $+1.00$ (extreme right handedness) to -1.00 (extreme left-handedness). We also classified participants as either consistent- or mixed-handers (Chiarello, Welcome, Halderman, & Leonard, 2009) based on their questionnaire responses; 103 reported no use of the non-dominant hand (consistent) and 97 reported at least some use of the non-dominant hand (mixed). More detailed demographic data on this sample are described in prior publications (Chiarello, Welcome, Halderman, & Leonard, 2009; Chiarello, Welcome, Halderman, Towler, et al., 2009; Leonard et al., 2008; Welcome et al., 2009), where it was noted that a range of reading skill was observed.

Behavioural stimuli and procedure

In an initial 2-hour session participants completed questionnaires regarding handedness, language and family background, reading history (Adult Reading History Questionnaire (AHRQ); Lefly & Pennington, 2000), and standardised measures of reading skill and intelligence (Wechsler, 1999; Woodcock, 1998). Following this session four test sessions were held on separate days in which participants completed seven lateralised word recognition tasks. All participants received tasks and test sessions in the same order.

Experimental stimuli consisted of three- to six-letter concrete nouns and/or pronounceable nonwords. Nonwords were created by replacing a single letter of a concrete noun, with each position of replacement occurring equally often. No stimuli were repeated within an experimental session, and no stimulus was used more than twice throughout the entire study. Word lists for each task were equated for word length and log-transformed word frequency based on the Hyperspace Analogue to Language corpus (Lund & Burgess, 1996). Mean word length for each task ranged from 4.44 to 4.64 and mean log word frequency ranged from 4.16 to 4.71. Within each task, items were matched across visual field conditions on the basis of length, log frequency (Lund & Burgess, 1996), familiarity (Wilson, 1988), and imageability (Wilson, 1988).

All stimuli were presented in upper case, black, 20-point Helvetica font on a white background on an Apple Studio Display M7649 monitor. Macintosh computers were used for stimulus presentation and recording of manual responses in the visual field tasks. Psyscope programming software (Cohen, MacWhinney, Flatt, & Provost, 1993) was used to control experimental events and record responses. Participants were seated 60 cm in front of the monitor, using a headrest to stabilise head position. For those experiments requiring manual responses (Lexical Decision, Masked Word Recognition, and Semantic Decision), participants used the index fingers of each hand on the "." and "x" keys to indicate one response and the middle fingers of each hand on the "/" and "z" keys to indicate the other response. This configuration was designed to accommodate both left- and right-handed participants. A Sony ECM-MS907 microphone was used to register vocal responses. Vocal responses were entered into the data file by an experimenter. Special codes were entered for spurious vocal responses (a cough, for example), or failure to respond, and such trials were not analysed.

The tasks were administered across four testing sessions, in the following order:

- *Lexical Decision*: 90 word and 90 nonword trials, key press discrimination response, 125-ms exposure.
- *Word Naming*: 90 trials, pronounce word, 125-ms exposure.
- *Category Generation*: 82 trials, produce exemplar of stimulus noun category (e.g., FRUIT), 155-ms exposure.
- *Nonword Naming*: 90 trials, pronounce nonword, 150-ms exposure.
- *Masked Word Recognition*: 100 trials, recognise word preceded and followed by 60-ms pattern mask (@#@#), two-alternative forced choice key press response, 30-ms exposure. The response alternatives differed by only a single letter.
- *Verb Generation*: 100 trials, produce verb associated with stimulus noun, 150-ms exposure.
- *Semantic Decision*: 120 trials, determine whether stimulus noun represents a naturally occurring or manmade object, key press response, 120-ms exposure.

On average, each session was separated by 4 days. Each task was preceded by 30–48 practice trials.

Stimuli were randomly presented to the left or right visual field (LVF, RVF), 1.8 degrees eccentric from a central fixation "+". At the onset of each trial the fixation marker appeared for 600–805 ms and flickered just prior to the onset of the stimulus. Participants were instructed to maintain central fixation and respond as quickly and accurately as possible.

Imaging procedure

After the images were reviewed for neuropathology they were transferred to compact discs at the Imaging Center and sent to the McKnight Brain Institute at the University of Florida. Preprocessing the images was performed using FSL scripts (http://www.fmrib.ox.ac.uk/) (Smith et al., 2004). Extraction of the brain parenchyma from scalp and skull was performed with BET (Smith, 2002) before registration (FLIRT) (Jenkinson

& Smith, 2001) to a 1-mm isovoxel study-specific template image aligned into the Talairach planes. No non-linear warping was performed on the images. Hence changes in the images were restricted to the translation and rotation necessary to align the midline and the anterior commissure–posterior commissure axis with the standard Talairach planes. Segmentation into separate grey matter, white matter, and cerebrospinal fluid (CSF) volumes was performed using FAST (Zhang, Brady & Smith, 2001). In these volumes each voxel is represented as a partial volume estimate of a particular tissue type. The volume of each tissue type was calculated by multiplying the number of voxels times the average partial volume estimate of those voxels as described on the FSL website. Volumes, surface areas, means, standard deviations, and average asymmetries were automatically accumulated in a data file for statistical analysis. Each structure was measured twice by at least two different investigators who were blind to hemisphere and participant characteristics. When there was more than 15% disagreement between the average values for the two measurements, the experimenters conferred and identified the reason for disagreement and then re-measured until the two measures agreed.

Grey matter, white matter, and cerebrospinal fluid (CSF) volumes of each hemisphere were estimated by outlining every fifth sagittal image starting at the midline. The brainstem was excluded by transection in the midcollicular plane. The midsection was traced twice and half the slab volume added to each hemisphere. The inter-rater reliability of this measure is $>.98$ (intraclass correlation). Preliminary studies showed that the accuracy of volumes sampled in this way was equivalent to that in which every section was measured.

Surface area of the planum temporale was calculated between $x = 47$ and 56 (sagittal coordinates adjusted for hemisphere width and chosen to maximise lateral asymmetry as well as reliability) (Chiarello et al., 2004; Eckert, Lombardino, & Leonard, 2001; Leonard et al., 1996). In individuals with one clearly defined Heschl's gyrus, the anterior border of the planum temporale was defined as the depth of the sulcus that formed the posterior border of Heschl's gyrus (Heschl's sulcus). When Heschl's gyrus is indented by an intermediate sulcus, the tracing includes the gyri on both banks of the sulcus. When an independent gyrus appears posterior to Heschl's gyrus, this gyrus is included in the planum measurement (Eckert, Leonard, Possing, & Binder, 2006). The posterior boundary of the planum temporale was defined as the origin of the posterior ascending ramus or the termination of the Sylvian fissure. Inter-rater reliability for these measurements is .85. Asymmetry coefficients for the planum temporale were calculated by subtracting the left measure from the right and dividing by the average, so that leftward asymmetries yielded positive coefficients. We observed reliable leftward asymmetry for the planum temporale in the current sample (see Chiarello, Welcome, Halderman, Towler, et al., 2009; Leonard et al., 2009). A comparative study of techniques to measure the planum temporale (Best & Demb, 1999) found that asymmetry measures using this index agreed well with those gained using other techniques.

The area of the corpus callosum was extracted from the midsagittal white matter image. It was subdivided into seven subdivisions (rostrum, genu, anterior, mid and posterior body, isthmus, and splenium) using the method of Witelson (1989). Because of the well-known relationship between corpus callosum area and overall cerebral volume, we controlled for the effects of cerebral volume through regression (Smith, 2005). Hence we report the residualised callosal area, which statistically eliminates the variance in callosal area that is due to brain size (see Welcome et al., 2009, for prior use of this measure in the current sample).

RESULTS

Data-analytic approach

Cluster analysis is an exploratory technique that identifies empirically determined groups of individuals who are similar to each other on a particular set of variables. This technique maximises within-cluster homogeneity and between-cluster heterogeneity (Hair & Black, 1998). We used Ward's Method, a hierarchical agglomerative procedure that identifies clusters in which the variance of cases within a cluster is relatively small. The distance metric is the sum of the squared distances of each individual's data from the mean of their cluster. This method is widely used in social science research (Romesburg, 1984).

Because variables that are strongly intercorrelated can be weighted more in cluster analyses, it is preferable to select measures that are not strongly correlated (Everitt, 1975; Hair & Black, 1998). We examined the intercorrelation matrices for our reading and lateralisation tasks, and selected as cluster variates those that were uncorrelated or only very weakly correlated. These represented both reading skill and DVF performance measures (both RT and accuracy) (average intercorrelation of the cluster variates = .076). Word attack scores showed the largest range of individual variation of the reading subtests, so this reading measure was included. The cluster variate asymmetry scores included both word identification and semantic tasks: masked word recognition (RT and accuracy), verb generation (RT and accuracy), lexical decision (RT and accuracy), and nonword naming RT. Based on our previous reliability analyses of various asymmetry indices

(Chiarello, Welcome, Halderman, Towler, et al., 2009), accuracy asymmetry was estimated by the lambda z-score (Bryden & Sprott, 1981) and RT asymmetry by the laterality index (LVF–RVF)/(LVF + RVF). To eliminate scaling differences across our measures, all data were *z*-scored before being entered into the cluster analysis (Hair & Black, 1998).

We first identified outliers from the multivariate dataset that included only the cluster variates, and then ran and examined the cluster analysis with outliers excluded. We next compared the clusters on reading/lateralisation task variables that were not used to create the clusters to examine the generalisability of the classification. Planar asymmetry and corpus callosum measurements were then compared across clusters to investigate potential neural correlates of the behavioural profiles. Although the outliers do not represent their own cluster, we also examined their data since it was predicted that individuals with atypical combinations of behavioural features might also have unusual reading or neuroanatomical profiles.

Findings

Multivariate outliers were identified from the set of cluster variates using the SAS OUTLIER macro (Friendly, 2003). The procedure calculates the robust Mahalnobis distances for each case in the data set, and identifies the probability that a given case belongs to any identifiable cluster. A total of 17 cases were identified as outliers (probability <.05 for cluster membership, d^2 values of 15.5 or above), and they were excluded from the cluster analysis. The SAS CLUSTER procedure (Ward's Method) was used to identify cluster solutions. As there was a large drop in the eigenvalues between the 5- and 6-cluster solutions (from .93 to .77), we examined the 3-, 4-, and 5-cluster solutions.

The 3-cluster solution (eigenvalue = 1.13) separated individuals into groups with low, high, or average word attack scores. On nearly all asymmetry measures, those with average word attack scores had larger RVF advantages than those with poor word attack scores. However, the asymmetries for those with high word attack scores did not show any discernable pattern relative to the other two groups. However, in the 4-cluster solution (eigenvalue = .97), the high word attack individuals split into two clusters, one with much smaller asymmetries than the others in all but one task measure. In the 5-cluster solution (eigenvalue = .93), those with average word attack scores split into two clusters; although these two new clusters differed significantly in asymmetry for several tasks, the direction of the differences was inconsistent (i.e., one cluster had larger RVF advantages for four task measures, and the other had larger RVF advantages for three task measures).

Based on these findings the 4-cluster solution appeared to be the most meaningful, accounting for 74% of the variance. Hence we adopted this solution. Table 1 displays the mean *z*-scores[2] for the cluster variates for each cluster, and the univariate *F* ratios that tested cluster differences for each variable. The F ratios indicated that all variables used in the cluster analysis successfully differentiated the clusters, verifying that none was a masking variable (Everitt, Landau, & Leese, 2001). Cluster 1 ($N = 61$) was characterised by very low word attack scores (for this sample), and VF asymmetries that were mostly smaller than average. The individuals in Cluster 2 ($N = 26$) had relatively high word attack scores and VF asymmetries that were uniformly near bottom of distribution, including some that were extremely low (masked word recognition and lexical decision accuracy, verb generation RT).[3] Cluster 3 ($N = 63$) was characterised by average word attack scores and, with the exception of masked word recognition, VF asymmetries that were quite large. Cluster 4 resembled Cluster 2 in having high word attack scores, but VF asymmetries that varied substantially over tasks—individuals in this cluster had the highest asymmetries in masked word recognition, average asymmetries in lexical decision, and reduced asymmetries for verb generation accuracy and nonword naming RT. For Cluster 4 the standard deviation for the cluster variate asymmetries was .495 (deviations for the other clusters were between .206 and .320).

Table 2 presents the *z*-scored means, and univariate *F* tests, for the additional reading and VF lateralisation measures that were not used in the cluster analysis. With the exception of the RT asymmetry for category generation, all of these measures differed by cluster. This indicates that the group differences identified in the cluster analysis generalise to additional reading and VF lexical tasks. Examination of the mean scores for each cluster confirms our original characterisation of the clusters. Cluster 1 individuals, who represented approximately 30% of the sample, performed most poorly on the other reading subtests and had low-to-average VF asymmetries. Cluster 2 individuals performed well on the reading measures and obtained consistently low VF asymmetries. Cluster 3 (approximately 32% of the sample) was characterised by near average reading skills and a

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[2] All data are reported as *z*-scores to facilitate comparisons across measures. A *z*-score of 0 represents the sample mean, hence negative *z*-scores are those falling below the mean. As reported previously (Chiarello, Welcome, Halderman, Towler, et al., 2009) all VF tasks, with the exception of nonword naming RT, resulted in robust RVF/LH advantages. Therefore a *z*-score of 0 for the VF measures indicates the typical RVF/LH advantage for that task; small negative *z*-scores indicate a reduced RVF/LH advantage and large negative *z*-scores a reversed asymmetry.

[3] Inspection of the untransformed asymmetries indicated that, for individuals in Cluster 2, 11 had reversed or no asymmetry for masked word recognition, 19 had reversed or no asymmetry for verb generation, and 3 had reversed asymmetry for lexical decision.

TABLE 1
Cluster *z*-score means (*SD*) and univariate *F* statistics for cluster variates

	Cluster 1 ($N=61$)	*Cluster 2* ($N=26$)	*Cluster 3* ($N=63$)	*Cluster 4* ($N=33$)	$F(3,179)$	η^2
Reading Skill:	Poorer	Good	Average	Good		
VF Asymmetry:	Low-to-average	Low	Large	Varies by task		
Reading Subtest						
Word Attack	−.748 (.634)	.851 (.547)	−.032 (.975)	.600 (.794)	34.9***	.37
Accuracy Asymmetry						
Masked Word Rec	.135 (.890)	−.715 (.836)	−.195 (.855)	.672 (.654)	15.3***	.20
Verb Generation	−.112 (.920)	−.164 (.659)	.358 (1.08)	−.430 (.792)	6.04***	.09
Lexical Decision	−.295 (.869)	−.777 (.731)	.505 (1.02)	.006 (.719)	15.7***	.21
RT Asymmetry						
Nonword Naming	−.106 (.607)	−.682 (.684)	.328 (.716)	−.279 (.734)	15.3***	.20
Masked Word Rec	−.356 (.608)	−.146 (.870)	−.197 (.912)	.937 (1.00)	18.8***	.24
Verb Generation	−.250 (.909)	−.703 (.898)	.338 (.942)	.253 (.978)	9.9***	.14
Lexical Decision	−.502 (.769)	−.379 (.730)	.607 (.745)	−.017 (.817)	24.1***	.29

**$p < .0001$.

tendency towards large VF asymmetries. Cluster 4 individuals demonstrated excellent reading skill, and variable VF asymmetries (although the differences across tasks were not as dramatic as for the cluster variates).

It is notable that not every possible combination of reading skill and VF lateralisation was observed. For example, there was no cluster of individuals with highly skilled reading and consistently large RVF/left hemisphere advantages, or with average reading ability and reduced VF asymmetry. Although, as discussed further below, there is no simple linear relationship between reading skill and visual lateralisation, this does not indicate that every possible relationship between these domains is observed.

We also examined whether the clusters could be differentiated by demographic variables (see Table 3). Chi-square analyses examined whether the categorical variables sex and mixed vs consistent handedness differed by cluster. Neither differed significantly by cluster: sex $\chi^2(3, N=183) = 5.51$, $p = .14$; mixed/consistent handedness $\chi^2(3, N=183) = 2.94$, $p = .40$. A more continuous measure of handedness, score on the inventory, also did not differ by cluster ($F < 1$). The clusters did not differ in socioeconomic status ($F < 1$), or self-reported history of reading problems as indexed by the ARHQ, $F(3, 177) = 1.48$, $p = .22$. However, there were some differences in mean age, $F(3, 179) = 5.02$, $p < .01$, $\eta^2 = .08$, verbal IQ, $F(3, 179) = 5.72$, $p < .001$, $\eta = .09$, and performance IQ, $F(3, 179) = 4.56$, $p < .01$, $\eta = .07$. Post-hoc contrasts (Tukey-Kramer adjustment) indicated that Cluster 1 individuals were younger ($M = 20.4$ yrs) than those in Clusters 2, ($M = 23.3$

TABLE 2
Cluster z-score means (SD) and univariate F statistics for non-cluster variates

	Cluster 1 (N = 61)	*Cluster 2 (N = 26)*	*Cluster 3 (N = 63)*	*Cluster 4 (N = 33)*	*F(3, 179)*	η^2
Reading Skill: VF Asymmetry:	Poorer Low-to-average	Good Low	Average Large	Good Varies by task		
Reading Subtest						
Word Identification	−.535 (.857)	.434 (.884)	.037 (.971)	.528 (.913)	12.7***	.19
Passage Compreh	−.382 (.912)	.376 (.867)	−.117 (1.07)	.362 (.882)	6.3**	.11
Accuracy Asymmetry						
Word Naming	−.047 (1.00)	−.635 (.911)	.398 (.902)	−.321 (1.01)	8.7***	.13
Categ Generation	−.048 (1.00)	−.280 (.881)	.316 (1.11)	−.325 (.808)	4.0*	.06
Nonword Naming	−.130 (.801)	−.328 (.936)	.434 (1.00)	−.270 (.889)	7.3***	.11
Semantic Decision	.247 (.891)	−.752 (.950)	.110 (1.02)	−.111 (.963)	7.1**	.11
RT Asymmetry						
Word Naming	−.335 (1.06)	−.608 (.795)	.428 (.931)	.068 (.820)	10.5***	.14
Categ Generation	.126 (1.08)	−.188 (.827)	−.074 (1.11)	.044 (.781)	< 1	.01
Semantic Decision	−.008 (.823)	−.434 (1.07)	.091 (.977)	.316 (1.00)	3.2*	.05

$^{***}p < .0001$, $^{**}p < .001$, $^{*}p < .05$.

yrs) $p = .002$, $d = 0.86$, and 3, ($M = 22.0$ yrs) $p = .047$, $d = 0.48$. Those in Cluster 1 also had lower verbal IQs ($M = 104.5$) than those in Clusters 2, ($M = 112.3$) $p = .01$, $d = 0.75$, and 4, ($M = 112.7$) $p = .003$, $d = 0.77$. Performance IQ was lower for Cluster 1 ($M = 105.2$) relative to Cluster 2 ($M = 113.5$), $p = .01$, $d = 0.76$. None of the other contrasts was significant.

To recap our behavioural findings, the cluster analysis identified four subtypes of individuals. One type (Cluster 1) showed poor performance on the reading and IQ measures and had small VF asymmetries. A second type (Cluster 3) showed average standardised test performance and large VF asymmetries. Two smaller subgroups of individuals showed good reading performance, and this was associated with either with low VF asymmetries (Cluster 2) or with variable task asymmetries (Cluster 4).

There were no differences between clusters in brain volume, $F(3, 179) = 1.30$, $p = .28$. Table 4 provides the means for each cluster for planum temporale asymmetry and the residualised corpus callosum measurements (in z-scores). Planum temporale asymmetry did not differ significantly by cluster. We did observe cluster differences for some of the callosal measurements (see Table 4). Although there were no differences for the entire corpus callosum area, or for the more anterior subregions, differences were observed for the posterior body and splenium. Post hoc contrasts indicated that the posterior body was significantly smaller for Cluster 4

TABLE 3
Demographic characteristics of clusters and unclassifiable individuals (outliers)

	Cluster 1 (N = 61)	*Cluster 2 (N = 26)*	*Cluster 3 (N = 63)*	*Cluster 4 (N = 33)*	*Outliers (N = 17)*
Mean Age (years)	20.4	23.3	22.0	21.6	22.1
Mean Hand Preference Score	+.677	+.696	+.725	+.661	+0.812
% Mixed (Left) Handed	45.9%	61.5%	46.0%	57.6%	29.4%
	(13.1%)	(11.5%)	(11.1%)	(9.1%)	(5.9%)
% Male	41.1%	61.5%	60.3%	45.5%	41.1%
Mean SES	3.16	3.37	3.47	3.33	3.29
VIQ	104.5	112.3	108.0	112.7	113.4
PIQ	105.2	113.5	107.2	111.6	114.8
Mean ARHQ	.316	.289	.292	.272	.302

individuals (good readers, task-dependent VF asymmetries), than for Cluster 1 individuals (poor readers, low/average VF asymmetries), $p = .004$, $d = 0.76$. Although it did not reach significance, a similar pattern was observed for the callosum midbody. Post-hoc contrasts for the splenium indicated that Cluster 2 individuals (good readers, reduced VF asymmetries) had larger splenia relative to Cluster 1 ($p = .02$, $d = 0.61$), Cluster 3 ($p = .03$, $d = 0.73$), and Cluster 4 ($p = .06$, $d = 0.68$).[4] Because Cluster 2 had the smallest number of cases, one might suspect that a few extreme scores in this group could unduly skew the mean. However, as Table 4 indicates, Cluster 2 actually had the smallest standard deviation in splenium size, rendering such an account implausible.

As noted earlier, 17 individuals were identified as multivariate outliers and could not be included in the cluster analyses. These outliers, then, have reading/VF asymmetry profiles on the cluster variates that are not characteristic of the rest of the sample and are not similar enough to each other to form another cluster. However, we examined their behavioural and neuroanatomical data to help understand why these individuals might be unusual and whether they might have atypical neuroanatomical features. Table 5 presents the means and standard deviations for the outliers for the reading subtests and for composite measures of overall VF asymmetry and consistency of asymmetry. The composite asymmetry score for each participant is the average of their z-scored asymmetries over all VF tasks, and the consistency of asymmetry is each participant's standard deviation of

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[4] As noted in a prior publication using this sample (Welcome et al., 2009), two male participants had extremely large corpus callosa. This raises the question as to whether the current findings might have been influenced by two highly unusual cases. When these two individuals were dropped from the current analyses, all of the reported effects remained significant. In fact the main effect for the splenium was more reliable, $F(3, 177) = 4.11$, $p = .008$, $\eta^2 = .07$, as were all post hoc contrasts (Cluster 2 vs 1, $p = .01$, $d = .70$, Cluster 2 vs 3, $p = .006$, $d = .81$, Cluster 2 vs 4, $p = .04$, $d = .69$).

TABLE 4
Mean (*SD*) Planum temporale (PT) asymmetry and residualised corpus callosum measurements (*z*-scores) by cluster

	Cluster 1 (N = 61)	*Cluster 2 (N = 26)*	*Cluster 3 (N = 63)*	*Cluster 4 (N = 33)*	*F(3, 179)*	η^2
Reading Skill:	Poorer	Good	Average	Good		
VF Asymmetry:	Low-to-average	Low	Large	Varies by task		
PT Asymmetry	.002 (.887)	.164 (1.04)	−.046 (1.12)	.180 (.984)	< 1	
Total Callosal Area	.062 (1.12)	.153 (1.00)	−.055 (.948)	−.212 (.932)	< 1	
Rostrum	.028 (.883)	−.093 (1.04)	−.027 (1.10)	−.075 (1.07)	< 1	
Genu	.097 (1.05)	−.165 (1.10)	.001 (.927)	−.078 (1.02)	< 1	
Anterior Body	−.030 (1.07)	.070 (1.04)	.066 (1.00)	−.051 (.955)	< 1	
Midbody	.191 (1.09)	.124 (.898)	−.041 (.946)	−.336 (.938)	2.19, $p = .09$	.04
Posterior Body	.224 (1.03)	−.059 (.940)	−.029 (.940)	−.478 (.789)	3.92**	.06
Isthmus	−.052 (1.19)	.097 (1.16)	−.016 (.847)	−.095 (.808)	< 1	
Splenium	−.068 (1.05)	.537 (.935)	−.146 (.937)	−.117 (.980)	3.28*	.05

**$p < .01$, *$p < .05$.

their asymmetry across measures (for previous use of these measures see Chiarello et al., 2004; Chiarello, Welcome, Halderman, Towler, et al., 2009). The latter measure of variation may be particularly important when examining atypical individuals, if their phenotype is more open to the effects of random variation. Because we wished to determine ways in which the outliers differed from the rest of the sample, *t*-tests were computed to make this comparison. In cases of unequal variances, adjusted *t*s and degrees of freedom were used.

With respect to the reading measures, outliers had unusually high passage comprehension scores, but not word-level reading scores (see Table 5). Their composite RT asymmetry provided evidence of larger RVF/LH advantages, relative to the rest of the sample, when combined across tasks. It is interesting to note that the outliers had much higher within-participant variability in their task asymmetries, especially for response time (see Table 5, consistency of VF asymmetry). This indicates that not only do the outliers fail to resemble identifiable subgroups in their reading/asymmetry profiles, but their individual asymmetries also vary more from task to task than do the rest of the sample—they show more extreme variation in VF asymmetry across tasks than was observed for the rest of the sample.

For contrasts involving demographic variables, the clustered and outlier participants did not differ by sex, age, handedness, socioeconomic status, or history of reading problems. However, the outliers had somewhat higher IQs, relative to the clustered individuals (VIQ, 113.4 vs 108.3), $t(198) = 1.85$, $p = .07$, $d = 0.48$; (PIQ, 114.8 vs 108.3), $t(198) = 2.27$, $p < .05$, $d = 0.64$.

TABLE 5
Comparison of clustered participants and outlier means (z-scores) for behavioural measures

	Clustered Subjects (N = 183)	*Outliers (N = 17)*	*t*	*d*
Reading Subtest				
Word Attack	−.031 (.982)	.337 (1.16)	1.45, *ns*	
Word Identification	−.009 (.996)	.092 (1.07)	<1	
Passage Comprehension	−.049 (.999)	.526 (.878)	2.29*	0.61
Composite VF Asymmetry				
Accuracy	−.011 (.536)	.124 (.670)	<1	
Response Time	−.023 (.451)	.249 (.504)	2.36*	0.57
Consistency of VF Asymmetry				
Accuracy	.851 (.251)	.999 (.326)	2.26*	0.51
Response Time	.851 (.277)	1.43 (.315)	8.15****	1.95

$*p < .05$; $****p < .00001$.

There was no difference in brain volume between the outliers and clustered individuals ($t < 1$). The outliers were less likely to have leftward asymmetry of the planum temporale, $t(198) = 1.89$, $p = .059$, $d = 0.51$. As a group their mean asymmetry did not differ from zero, $t(16) = 1.34$, $p = .20$. In comparison, the clustered individuals as a whole, and every separate cluster, showed leftward planar asymmetries that significantly differed from zero: Cluster 1, $t(60) = 6.31$, $p < .0001$; Cluster 2, $t(25) = 4.32$, $p < .0002$; Cluster 3, $t(62) = 4.75$, $p < .0001$; Cluster 4, $t(32) = 5.22$, $p < .0001$. Inspection of the untransformed asymmetries indicated that 41.2% of the outliers had larger right than left PT (compared to 19.7% for the individuals who

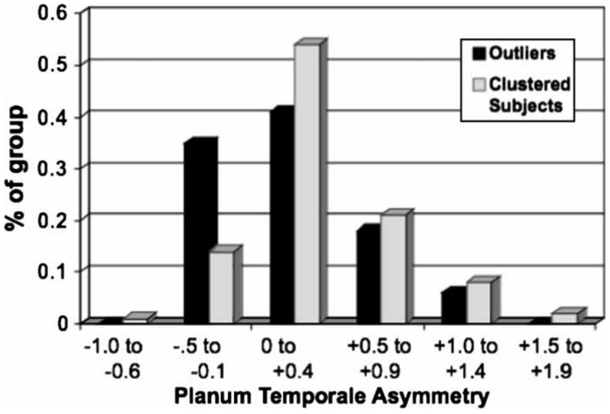

Figure 1. Distribution of planum temporale asymmetry (untransformed) for multivariate outliers vs clustered participants. Positive values indicate leftward asymmetry.

were successfully assigned to one of the four clusters), see Figure 1. When corrected for hemispheric grey matter volume, the outliers' left planum did not differ from that of the rest of the sample ($t < 1$), while their right planum was significantly larger, $t(198) = 2.14$, $p < .05$, $d = 0.30$. Although several callosal subregions were larger for the outliers (rostrum, posterior body, isthmus) these differences did not reach significance.

DISCUSSION

To summarise our major findings, the cluster analysis identified four subgroups with differing reading/VF lateralisation profiles. The clusters did not differ by sex or handedness, suggesting that there is identifiable behavioural variance between individuals that is not captured by standard participant variables. Although these groups had similar planar asymmetries, some group differences were observed in posterior callosal areas, as discussed further below. A small portion of the sample was identified as multivariate outliers with respect to the variables used in the cluster analysis. These individuals were notable for their high passage comprehension scores and highly variable VF asymmetries. Interestingly they also had an unusual distribution of planum temporale asymmetry. These results suggest that alternate quantitative approaches to the investigation of individual differences in brain–behaviour relations have promise.

We begin by interpreting the differences between the four clusters and then discuss the ways in which the multivariate outliers differ from those with more predictable reading/VF asymmetry profiles. After considering the strengths and limitations of this study, we conclude by suggesting a novel framework for interpreting individual differences in brain–behaviour relations.

Interpretation of clusters

In characterising the differences between the clusters, we consider all our variables, not just those used to create the clusters. Cluster 1 individuals ($N = 61$) performed most poorly on all reading subtests, and their verbal IQ was significantly lower than for the two good reader clusters (2 and 4). Their VF asymmetries ranged from average to below average, but their planar asymmetry and corpus callosum measurements were not unusual in any way. This group appears to be low in verbal skills, relative to our college population, but we observed no particular neuroanatomical marker associated with this behavioural profile. Since neither their VF, nor their planar, asymmetry was the lowest for our sample, they do not provide evidence for an association between poor reading and lack of asymmetry (for review of this controversy see Leonard & Eckert, 2008). Cluster 3 individuals ($N = 63$), in contrast, were quite average readers, and with the exception of one task (masked word recognition), they had exaggerated RVF/LH advantages on our verbal tasks. Masked word recognition differs from the other tasks in that it places high demands on the ability to rapidly extract visual information necessary for word recognition, and engaging in this process apparently involves more bilateral processing for persons in this cluster. However, although this group had the largest asymmetries for most tasks, their neuroanatomical measurements were quite typical for the sample. In this sample, then, the direction/degree of planar asymmetry did not distinguish among college student readers with average or below average reading skill.

Individuals in Clusters 2 ($N = 26$) and 4 ($N = 33$) were highly skilled readers, as evidenced by their scores across all the reading subtests. They differed, however, in their VF asymmetries and in callosal measurements. Cluster 2 was characterised by consistently small VF asymmetries, and interestingly, very large splenia. The splenium area for this group was significantly larger than for all other clusters. These findings are consistent with the idea that reduced task asymmetries are associated with a greater degree of interhemispheric communication. Because the splenium connects visual processing areas, this may explain the association of this callosal region with performance in our divided visual field tests. Some have argued that mixed-handers have a greater degree of interhemispheric communication than consistent-handers (Christman, Jasper, Vralakshmi, & Cooil, 2007; Christman, Propper, & Dion, 2004). To the extent that callosal area indexes facility of interhemispheric communication, our findings do not support this view, as the clusters did not differ by any measure of handedness. The VF and callosal data for Cluster 2 do suggest an association between large splenia and reduced visual, but not manual, asymmetry.

Cluster 4 individuals also had strong reading scores but a more complex pattern of VF asymmetries, characterised by extremely large masked word recognition asymmetry, reduced asymmetry for nonword naming, and average asymmetry for lexical decision. Most VF measures indicated larger RVF/LH advantages for Cluster 4 individuals, as compared to the good readers of Cluster 2. The posterior body of the corpus callosum was smallest for Cluster 4 individuals. It is interesting that differences in (posterior) callosal areas were only observed for the clusters with highly skilled readers, with an association between reduced VF asymmetry and enlarged splenia (Cluster 2) and larger (although variable) VF asymmetry and reduced callosal posterior body (Cluster 4). Prior studies of the relation between callosal area and reading ability have contrasted normal and dyslexic readers (see review in Fine, Semrud-Clikeman, Keith, Stapleton, & Hynd, 2007), but cannot inform us about callosal morphology among highly skilled readers, whereas studies of language lateralisation and callosal size have not investigated reading skill effects (e.g., Westerhausen et al., 2006). The corpus callosum continues to mature well into adulthood (Pujol, Vendrell, Junque, Marti-Vilalta, & Capdevila, 1993), with extended maturation for posterior areas, particularly the splenium, as indicated by age-dependent variations in macrostructure (Giedd et al., 1999), axonal organisation evident from diffusion tensor imaging (Li & Noseworthy, 2002; Muetzel et al., 2008), and behaviour (Muetzel et al., 2008). The most proficient readers will have accumulated greater reading experience during this later maturation period, perhaps increasing the probability of experience-dependent sculpting of callosal organisation relevant to reading processes. One can speculate that these skilled readers continue to "fine tune" the relationship between hemispheric specialisation for reading and interhemispheric channels, resulting in associations between lateralisation and callosal area that are not found in less skilled readers. However, given the exploratory nature of the current study, this suggestion should be regarded as highly speculative.

In general, the cluster analysis findings suggest that a variety of reading/lateralisation profiles exist among college-age readers, and that these cannot be accounted for by variations in standard grouping variables such as sex or handedness. In addition, this bottom-up approach revealed associations between reading skill and VF lateralisation that could be obscured by correlational approaches. For example, although the clusters differed in reading skill this was not related to VF lateralisation for word reading in a linear way: uniformly small VF asymmetries were observed in one group of skilled readers, moderately small or variable asymmetries were observed in both another group of skilled readers and in poorer readers, while the largest VF asymmetries were found to characterise those with average reading skill. In addition, although the clusters were determined based on behavioural data alone, variations in posterior corpus callosum anatomy were observed, implying that clusters of traits related to reading can be associated with particular neural substrates.

Characteristics of multivariate outliers

A minority of individuals in our sample had reading and VF asymmetry profiles that differed substantially from the rest of the sample. This suggests that their performance departed in idiosyncratic ways from the "normative" profiles identified by the cluster analysis. In an effort to understand what made these individuals unusual we compared their behavioural and neuroanatomical findings to the rest of the sample. Some intriguing results were observed. First, the outliers had significantly higher passage comprehension scores than the clustered individuals, yet their word level reading ability was unremarkable. This contrasts to those in clusters 1–4 whose word- and text-level reading skills were quite similar (see Table 1 & 2). This could indicate that the outliers achieve superior comprehension via increased reliance on top-down context information that is available for text, but not single word, reading. The higher IQs of the outliers are consistent with this interpretation, as greater world knowledge and reasoning abilities could serve to enhance comprehension independent of word identification skill (cf. Chiarello, Lombardino, Kacinik, Otto, & Leonard, 2006). Second, the outliers tended to have greater RT, but not accuracy, asymmetries than the rest of the sample (see Table 5, Composite VF Asymmetry). This decoupling of RT and accuracy asymmetry was not observed for the combined cluster group, nor for any individual cluster. Third, both accuracy and especially RT asymmetries were very inconsistent from task to task for the individuals identified as outliers relative to the rest of the sample (see Table 5, Consistency of VF Asymmetry). In other words, these individuals had very large discrepancies in the size and direction of their VF asymmetry indices across tasks, for both response measures.[5]

In general, then, the behavioural outcomes for the outliers were characterised by dissociations between measures that tended to covary for the rest of the sample: between word- and text-level reading ability, between RT and accuracy asymmetry, and between VF asymmetries across various lexical tasks. This explains, at least partially, why these individuals were statistically identified as outliers relative to the rest of the sample. Conceptually, these dissociations suggest a less regulated form of behavioural development, at least for abilities related to reading.

A biological framework for such an outcome is provided by the concept of buffering, that is, reduced sensitivity of phenotypes to genetic and environmental influences during development (Salazar-Ciudad, 2007). This view is based on current research in developmental biology suggesting that a complex genetic network regulates developmental processes that serve to buffer the organism from random influences (Rice, 2008; Siegal & Bergman, 2002). The net effect of this regulation is "canalisation"; that is, silencing of genetic variation and regression towards the population mean, as originally suggested many decades ago (Waddington, 1957). In other words, individuals with a greater degree of buffering will have more "typical" phenotypes. This more contemporary research (e.g., Landry, 2009; Salathia & Queitsch, 2007) provides a molecular basis for the earlier concept of developmental instability (Markow, 1994; Yeo, Gangestad, & Daniel, 1993). It is important to note that individuals will differ in the effectiveness of regulation (Jaenisch & Bird, 2003; Rasmuson, 2002). We hypothesise that the "outliers" identified

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[5] Cluster 4 individuals also had somewhat variable asymmetries. However, the average asymmetry standard deviations (consistency scores across all seven VF tasks) for these individuals (accuracy asymmetry $SD = .858$, RT asymmetry $SD = .886$) were similar to the other clusters and smaller than those observed for the outliers.

in our study may have a less buffered type of development that is more open to the effects of random genetic and environmental perturbations. Random genetic/environmental influences could have both positive and negative effects on behavioural outcomes in individuals with less regulated, more plastic development (Belsky & Pluess, 2009). In our sample the outliers generally had superior intelligence and reading comprehension. This may be due to the fact that our sample was drawn from a university community. In contrast, dysregulated individuals who had been subjected to primarily negative environmental and genetic influences might be much less likely to develop the cognitive and linguistic abilities needed to attend college, and hence not be represented in our sample population. Clearly a sample that is more representative of the general population will be needed to examine this conjecture.

The pattern of planar asymmetries observed for the outliers is consistent with the dysregulation view. Within this framework development of the right and left hemisphere would be coordinated in individuals with high degrees of epigenetic regulation, resulting in modal asymmetries. Relative to the rest of the sample, the outliers were more likely to have reversed (rightward) planum temporale asymmetry (Figure 1), with the reduction of asymmetry due to increased size of the typically smaller structure in the right hemisphere. It is notable that asymmetry for the planum temporale is typically very robust, having been replicated in numerous studies (Shapleske et al., 1999; Sommer et al., 2008). Because the outliers were identified as unusual based only on their behavioural findings, it is quite interesting that they were also unusual in neuroanatomy.

Finally we note that findings from the outliers provide counterevidence for the view that dyslexia or impaired reading is associated reduced or reversed planar asymmetry (Leonard & Eckert, 2008). This group did not show the expected leftward planar asymmetry, yet their reading comprehension was superior. Hence the current data imply that poor reading is not a necessary correlate of unusual planar asymmetries.

Strengths and limitations

An important strength of the current investigation is the large sample size that allowed us to examine a range of behavioural and neuroanatomical variation within a population of normal readers. We were also able to assess groupings based on clusters of behavioural traits instead of relying on a priori groups based on a single behavioural measure (Golestani et al., 20078; Prat et al., 2007). Furthermore, this method allowed us to investigate individuals who did not fit into any behaviourally defined group (i.e., outliers), rather than having such persons contribute to “error variance”. To the extent that our bottom-up approach produced meaningful behaviourally defined groups, we could begin to investigate dimensions of individual difference that have not emerged using more traditional methodological approaches.

However we note that our sample, although large, cannot represent the extent of variation present in population as a whole. Because all participants were college students, individuals with the lowest levels of ability, achievement, or socioeconomic opportunity were not adequately represented. As noted above, this prevented us from investigating potentially dysregulated individuals whose environmental/genetic influences might have resulted in negative outcomes. A much broader, community-based sample would be needed to fully exploit the range of variation present in the population as a whole. Yet even with our restricted sample we observed extensive behavioural and neuroanatomical variability. The small number of left-handers in the sample also limits our ability to address issues regarding the direction (as opposed to degree) of handedness. Additional research that over-samples the left-handed population will be required to investigate structural/functional correlates of handedness direction.

Another limitation concerns our methods for assessing brain structure and function. We relied on corpus callosum area measurements that cannot reveal variations in axonal integrity or connectivity. Investigations using diffusion tensor imaging are needed to more fully explore individual differences in callosal connectivity. The planum temporale measure relied on sulcal boundaries that do not necessarily indicate cytoarchitectural borders (Fischl et al., 2008), although these measurements have been shown to predict behaviour in a number of studies (e.g., Eckert et al., 2008; Leonard et al., 1996). Finally, the VF method is a very indirect way to assess functional lateralisation, although it does permit assessment of multiple tasks from a large sample. Ideally what is needed is functional imaging performed in a way that takes into account individual variation in brain structure (e.g., Crosson et al., 1999; Devlin & Poldrack, 2007), so that variations in behaviour, structure, and regional brain activity can be examined concurrently.

Characterising individual differences in brain–behaviour relations

Interest in individual differences often stems from a desire to understand what makes each of us unique. Yet, paradoxically, we must scientifically explore this issue by exploiting similarities among persons, either by treating each person as a single point on a continuum of variation (regression approach) or by combining individuals that are similar in some way into subgroups. The cluster analysis method employed here is simply a way to identify subgroups that makes fewer assumptions about the dimensions along which individuals should differ. The data we report suggest that this approach can reveal some interesting variations in reading skill, lateralisation, and brain structure that might not be evident using other methods. However, it is important not to reify the particular subgroups identified by this analysis. Had we entered different measures into the cluster analysis, different subdivisions within our sample would no doubt have been observed. Because each individual differs from others on a nearly infinite variety of dimensions, there will be many ways in which this multidimensional space can be partitioned. We make no claim that the way we partitioned this space in the current investigation is necessarily more valid than another.

To illustrate this point, consider the relationship between reading ability and lateralisation (structural and functional). A continuing question for neuropsychological investigations of reading is whether or not reduced or reversed cerebral asymmetry represents a risk factor for reading acquisition (Leonard & Eckert, 2008), and whether variations in adult reading skill covary with lateralisation differences (Chiarello, Welcome, Halderman, & Leonard, 2009). In a previous publication on the current sample we reported significant positive correlations between reading skill and VF lexical lateralisation, but only for those with consistent handedness (Chiarello, Welcome, Halderman, & Leonard, 2009). The correlations for consistent handers were quite modest (approximately .24) but suggested that, for those with strongly expressed handedness, better reading was associated with larger RVF/left hemisphere advantages. Yet in the current paper using the same sample we report four subgroups characterised by differing reading/VF lateralisation profiles. The groups did not differ by any measure of handedness, and the cluster with the largest RVF advantages had average (for our sample) reading skill. The most skilled readers (Clusters 2 and 4) did not have the greatest VF asymmetries. Because both sets of findings were obtained from the same sample, we cannot attribute the differing results to different experimental methods or demographic characteristics. Rather, we think that we have observed different ways of carving up the same multidimensional individual difference space. Note that even for consistent handers only approximately 6% of the variance in reading was accounted for by variations in VF lateralisation (Chiarello, Welcome, Halderman, & Leonard, 2009). At least some of this unexplained variance is likely due to the group differences uncovered by the current cluster analysis.

A visual metaphor may help to clarify this situation. When looking through a kaleidoscope we can perceive a succession of different visual patterns by rotating the kaleidoscope tube that adjusts a set of internal mirrors. The elements producing these patterns (coloured beads) do not change as the tube is rotated, and none of the resulting patterns is a truer reflection of the elements than any other. Yet a multitude of different patterns can be observed. Similarly, as investigators we strive to find patterns in the variations we observe between individuals. The patterns we can observe depend on the settings we have selected for our analytical lens (i.e., the variables and statistical methods we select). Only by continually rotating the tube (i.e., varying our variables and methods) can we hope to understand the many ways in which individuals are similar and different. It is likely that by so doing we will uncover a variety of ways in which the human brain can support cognitive functions such as reading.

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REFERENCES

Belsky, J., & Pluess, M. (2009). The nature (and nurture?) of plasticity in early human development. *Perspectives on Psychological Science*, *4*, 345–351.

Best, M., & Demb, J. (1999). Normal planum temporale asymmetry in dyslexics with a magnocellular deficit. *Neuroreport*, *10*, 607–612.

Bryden, M. P. (1982). *Laterality: Functional asymmetry in the normal brain*. New York: Academic Press.

Bryden, M. P., & Sprott, D. A. (1981). Statistical determination of degree of laterality. *Neuropsychologia*, *19*, 571–581.

Cherney, L. R., & Small, S. L. (2006). Task-dependent changes in brain activation following therapy for nonfluent aphasia: Discussion of two individual cases. *Journal of the International Neuropsychological Society*, *12*, 828–842.

Chiarello, C., Kacinik, N., Manowitz, B., Otto, R., & Leonard, C. (2004). Cerebral asymmetries for language: Evidence for structural–behavioural correlations. *Neuropsychology*, *18*, 219–231.

Chiarello, C., Lombardino, L. J., Kacinik, N. A., Otto, R., & Leonard, C. M. (2006). Neuroanatomical and behavioural asymmetry in an adult compensated dyslexic. *Brain and Language*, *98*, 169–181.

Chiarello, C., Welcome, S. E., Halderman, L. K., & Leonard, C. M. (2009). Does degree of asymmetry relate to performance? An investigation of word recognition and reading in consistent and mixed handers. *Brain and Cognition*, *69*, 521–530.

Chiarello, C., Welcome, S. E., Halderman, L. K., Towler, S., Julagay, J., Otto, R., et al. (2009). A large-scale investigation of lateralisation in cortical anatomy and word reading: Are there sex differences? *Neuropsychology*, *23*, 210–222.

Christman, S. D., Jasper, J. D., Varalakshmi, S., & Cooil, B. (2007). Individual differences in risk perception versus risk taking: Handedness and interhemispheric interaction. *Brain and Cognition*, *63*, 51–58.

Christman, S. D., Propper, R. E., & Dion, A. (2004). Increased interhemispheric interaction is associated with decreased false memories in a verbal converging semantic associates paradigm. *Brain and Cognition*, *56*, 313–319.

Christman, S. D., Vralakshmi, S., & Jasper, J. D. (2009). Individual differences in ambiguous-figure perception: Degree of handedness and interhemispheric interaction. *Perception*, *38*, 1183–1198.

Cohen, J. D., MacWhinney, B., Flatt, M., & Provost, J. (1993). PsyScope: A new graphic interactive environment for designing psychology experiments. *Behavioural Research Methods, Instruments, and Computers*, *25*, 257–271.

Colcombe, S.J., Kramer, A.F., Erickson, K.I., & Scalf, P. (2005). The implications of cortical recruitment and brain morphology for individual differences in inhibitory function in aging humans. *Psychology and Aging*, *20*, 363–375.

Crosson, B., Sadek, J. R., Bobholz, J. A., Gokcay, D., Mohr, C. M., Leonard, C. M., et al. (1999). Activity in the paracingulate and cingulate sulci during word generation: An fMRI study of functional anatomy. *Cerebral Cortex*, *9*, 307–316.

Devlin, J. T., & Poldrack, R. A. (2007). In defense of tedious anatomy. *NeuroImage*, *37*, 1033–1041.

Eckert, M. A., Leonard, C. M., Possing, E. T., & Binder, J. R. (2006). Uncoupled leftward asymmetries for planum morphology and functional language processing. *Brain and Language*, *87*, 102–111.

Eckert, M. A., Lombardino, L. J., & Leonard, C. M. (2001). Planar asymmetry tips the phonological playground and environment raises the bar. *Child Development*, *72*, 988–1002.

Eckert, M. A., Lombardino, L. J., Walczak, A. R., Bonihla, L., Leonard, C. M., & Binder, J. R. (2008). Manual and automated measures of superior temporal gyrus asymmetry: Concordant structural predictors of verbal ability in children. *NeuroImage*, *41*, 813–822.

Everitt, B. S. (1995). *Cluster analysis.* New York: Halsted Press.

Everitt, B. S., Landau, S., & Leese, M. (2001). *Cluster analysis* (4th ed.). London: Oxford University Press.

Fine, J. G., Semrud-Clikeman, M., Keith, T. Z., Stapleton, L. M., & Hynd, G. W. (2007). Reading and the corpus callosum: An fMRI family study of volume and area. *Neuropsychology*, *21*, 235–241.

Fischl, B., Rajendran, N., Busa, E., Augustinack, J., Hinds, O., Yeo, B. T., et al. (2008). Cortical folding patterns and predicting cytoarchitecture. *Cerebral Cortex*, *18*, 1973–1980.

Forstmann, B. U., Jahfari, S., Scholte, H. S., Wolfensteller, U., van den Wildenberg, W. P. M., & Ridderinkhof, K. R. (2008). Function and structure of the right inferior frontal cortex predict individual differences in response inhibition: A model-based approach. *Journal of Neuroscience*, *28*, 9790–9796.

Friendly, M. (2003). *SAS macro programs for statistical graphics: OUTLIER*. Retrieved from http://www.math.yorku.ca/SCS/sssg/outlier.html

Ganis, G., Thompson, W. L., & Kosslyn, S. M. (2005). Understanding the effects of task-specific practice in the brain: Insights from individual-differences analyses. *Cognitive, Affective, & Behavioural Neuroscience*, *5*, 235–245.

Giedd, J. N., Blumenthal, J., Jeffries, N. O., Rajapakse, J. C., Vaituzis, A. C., Liu, H., et al. (1999). Development of the human corpus callosum during childhood and adolescence: A longitudinal MRI study. *Progress in Neuro-Psychopharmacology and Biological Psychiatry*, *23*, 571–588.

Golestani, N., Molko, N., Dehaene, S., LeBihan, D., & Pallier, C. (2007). Brain structure predicts the learning of foreign speech sounds. *Cerebral Cortex*, *17*, 575–582.

Hair, J. F., & Black, W. C. (1998). Cluster analysis. In J. R. Hair, R. E. Andeson, R. L. Tatham, & W. C. Black (Eds.), *Multivariate data analysis* (pp. 469–518). Upper Saddle River, NJ: Prentice-Hall.

Harrington, G. S., & Tomaszewski, S. (2008). Sex differences in language processing: Functional MRI methodological considerations. *Journal of Magnetic Resonance Imaging*, *27*, 1221–1228.

Hellige, J. B., Taylor, K. B., Lesmes, L., & Peterson, S. (1998). Relationships between brain morphology and behavioural measures of hemispheric asymmetry and interhemispheric interaction. *Brain and Cognition*, *36*, 158–192.

Jaenisch, R., & Bird, A. (2003). Epigenetic regulation of gene expression: How the genome integrates intrinsic and environmental signals. *Nature Genetics*, *33(Suppl.)*, 245–254.

Jenkinson, M., & Smith, S. M. (2001). A global optimisation method for robust affine registration of brain images. *Medical Image Analysis*, *5*, 143–156.

Kaiser, A., Kuenzli, E., Zappatore, D., & Nitsch, C. (2007). On females' and males' bilateral activation during language production: A fMRI study. *International Journal of Psychophysiology*, *63*, 192–198.

Kosslyn, S. M., Cacioppo, J. T., Davidson, R. J., Hugdahl, K., Lovallo, W. R., Spiegel, D., et al. (2002). Bridging psychology and biology: The analysis of individuals in groups. *American Psychologist*, *57*, 341–351.

Landry, C.R. (2009). Systems biology spins off a new model for the study of canalization. *Trends in Ecology and Evolution*, *24*, 63–66.

Lefly, D. L., & Pennington, B. F. (2000). Reliability and validity of the adult reading history questionnaire. *Journal of Learning Disabilities*, *33*, 286–296.

Leonard, C. M., & Eckert, M. A. (2008). Asymmetry and dyslexia. *Developmental Neuropsychology*, *33*, 663–681.

Leonard, C. M., Lombardino, L. J., Mercado, L. R., Rowd, S. R., Brier, J. I., & Agee, O. F. (1996). Cerebral asymmetry and cognitive development in children: A magnetic resonance imaging study. *Psychological Science*, *7*, 79–85.

Leonard, C. M., Towler, S. D., Welcome, S., & Chiarello, C. (2009). Paracingulate asymmetry in anterior and midcingulate cortex: Sex differences and the effect of measurement technique. *Brain Structure and Function*, *213*, 553–569.

Leonard, C. M., Towler, S., Welcome, S., Halderman, L. K., Otto, R., et al. (2008). Size matters: Cerebral volume influences sex differences in neuroanatomy. *Cerebral Cortex*, *18*, 2920–2931.

Li, T-Q., & Noseworthy, M. D. (2002). Mapping the development of white matter tracts with diffusion tensor imaging. *Developmental Science*, *5*, 293–300.

Lund, K., & Burgess, C. (1996). Producing high-dimensional semantic spaces from lexical co-occurrence. *Behaviour Research Methods, Instruments, & Computers*, *28*, 203–208.

Markow, Jf (Ed.). (1994). *Developmental instability: Its origins and evolutionary implications* (pp. 299–308). Dordrecht, The Netherlands: Kluwer Academic.

Muetzel, R. L., Collins, P. F., Mueller, B. A., Schissel, A. M., Lim, K. O., & Luciana, M. (2008). The development of the corpus callosum microstructure and associations with bimanual task performance. *NeuroImage*, *39*, 1918–1925.

Narr, K. L., Bilder, R. M., Luders, E., Thompson, P. M., Woods, R. P., Robinson, D., et al. (2007). Asymmetries of cortical shape: Effects of handedness, sex, and schizophrenia. *NeuroImage*, *34*, 939–948.

Peterson, C. K., Gable, P., & Harmon-Jones, E. (2008). Asymmetrical frontal ERPs, emotion, and behavioural approach/inhibition sensitivity. *Social Neuroscience*, *3*, 113–124.

Prat, C. S., Long, D. L., & Baynes, K. (2007). The representation of discourse in the two hemispheres: An individual differences investigation. *Brain and Language*, *100*, 283–294.

Propper, R. E., Christman, S. D., & Phaneuf, K. A. (2005). A mixed-handed advantage in episodic memory: A possible role of interhemispheric interaction. *Memory & Cognition*, *33*, 751–757.

Pujol, J., Vendrell, P., Junque, C., Marti-Vilalta, J. L., & Capdevila, A. (1993). When does human brain development end? Evidence of corpus callosum growth up to adulthood. *Annals of Neurology*, *34*, 71–75.

Rasmuson, M. (2002). Fluctuating asymmetry: Indicator of what? *Hereditas*, *136*, 177–183.

Rice, S. H. (2008). Theoretical approaches to the evolution of development and genetic architecture. *Annals of the New York Academy of Sciences*, *1133*, 67–86.

Romesberg, H. C. (1984). *Cluster analysis for researchers.* Belmont, CA: Lifetime Learning Publications.

Salathia, N., & Queitsch, C. (2007). Molecular mechanisms of canalization: Hsp90 and beyond. *Journal of Bioscience*, *32*, 457–463.

Salazar-Ciudad, I. (2007). On the origins of morphological variation, canalization, robustness, and evolvability. *Integrative and Comparative Biology*, *47*, 390–400.

Shapleske, J., Rossell, S. L., Woodruff, P. W. R., & David, A. S. (1999). The planum temporale: A systematic, quantitative review of its structural, functional and clinical significance. *Brain Research Reviews*, *29*, 26–49.

Siegal, M. L., & Bergman, A. (2002). Waddington's canalization revisited: Developmental stability and evolution. *Proceedings of the National Academy of Sciences, USA*, *99*, 10528–10532.

Smith, R. J. (2005). Relative size versus controlling for size. *Current Anthropology*, *46*(2), 249–273.

Smith, S. M. (2002). Fast robust automated brain extraction. *Human Brain Mapping*, *17*, 143–155.

Smith, S. M., Jenkinson, M., Woolrich, M. W., Beckmann, C. F., Behrens, T. E. J., Johansen-Berg, H., et al. (2004). Advances in functional and structural MR image analysis and implementation in FSL. *NeuroImage*, *23*, 208–219.

Sommer, I. E., Aleman, A., Somers, M., Boks, M. P., & Kahn, R. S. (2008). Sex differences in handedness, asymmetry of the planum temporale and functional language lateralisation. *Brain Research*, *1206*, 76–88.

Sommer, I. E. C., Aleman, A., Bouma, A., & Kahn, R. S. (2004). Do women really have more bilateral language representation than men? A meta-analysis of functional imaging studies. *Brain*, *127*, 1845–1852.

Waddington, C. H. (1957). *The strategy of the genes*. London: George Allen & Unwin.

Wallentin, M. (2009). Putative sex differences in verbal abilities and language cortex: A critical review. *Brain and Language*, *108*, 175–183.

Wechsler, D. (1999). *Wechsler Abbreviated Scale of Intelligence*. San Antonio, TX: The Psychological Corporation.

Welcome, S. E., Chiarello, C., Towler, S., Halderman, L. K., Otto, R. J., & Leonard, C. M. (2009). Behavioral correlates of corpus callosum size: Anatomical/behavioral relationships vary across sex/handedness groups. *Neuropsychologia*, *47*, 2427–2435.

Westerhausen, R., Kreuder, F., Dos Santos Sequeira, S., Walter, C., Woerner, W., Wittling, R.A., et al. (2006). The association of macro- and microstructure of the corpus callosum and language lateralisation. *Brain and Language*, *97*, 80–90.

Wilson, M. D. (1988). The MRC Psycholingusitic Database: Machine readable dictionary, version 2. *Behavioural Research Methods, Instruments, and Computers*, *20*(1), 6–11.

Witelson, S. F. (1989). Hand and sex differences in the isthmus and genu of the human corpus callosum. A postmortem morphological study. *Brain*, *112*(Pt 3), 799–835.

Woodcock, R. W. (1998). *Woodcock Reading Mastery Test–Revised Normative Update (WRMT–R)*. Circle Pines, MN: American Guidance Service, Inc.

Yeo, R. A., Gangestad, S. W., & Daniel, W. F. (1993). Hand preference and developmental instability. *Psychobiology*, *21*, 161–168.

Zaidel, E., & Iacaboni, M. (2003). *The parallel brain: The cognitive neuroscience of the corpus callosum*. Cambridge, MA: MIT Press.

Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. *IEEE Trans Med Imaging*, *20*, 45–57.