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Behavioral correlates of corpus callosum size: Anatomical/behavioral relationships vary across sex/handedness groups

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ABSTRACT

There are substantial individual differences in the size and shape of the corpus callosum and such differences are thought to relate to behavioral lateralization. We report findings from a large scale investigation of relationships between brain anatomy and behavioral asymmetry on a battery of visual word recognition tasks. A sample of 200 individuals was divided into groups on the basis of sex and consistency of handedness. We investigated differences between sex/handedness groups in callosal area and relationships between callosal area and behavioral predictors. Sex/handedness groups did not show systematic differences in callosal area or behavioral asymmetry. However, the groups differed in the relationships between area of the corpus callosum and behavioral asymmetry. Among consistent-handed males, callosal area was negatively related to behavioral laterality. Among mixed-handed males and consistent-handed females, behavioral laterality was not predictive of callosal area. The most robust relationship was observed in mixed-handed females, in whom behavioral asymmetry was positively related to callosal area. Our study demonstrates the importance of considering brain/behavior relationships within sub-populations, as relationships between behavioral asymmetry and callosal anatomy varied across subject groups.

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1. Introduction

There are substantial individual differences in the size and shape of the corpus callosum. Behavioral correlates of this variation have long been sought. Because the callosum is the major fiber tract connecting the cerebral hemispheres, it is logical to suppose that individual differences in callosal morphology relate to individual differences in lateralization, the degree to which the left and right cerebral hemispheres differ. Prior studies have compared callosal morphology between groups thought to differ in lateralization, including groups defined by their sex (reviewed by Bishop & Wahlsten, 1997) or handedness (Preuss et al., 2002; Witelson & Goldsmith, 1991). Other studies have more directly attempted to identify relationships between behavioral asymmetry and callosal area (Hines, Chiu, McAdams, Bentler, & Lipcamon, 1992; Moffat, Hampson, & Lee, 1998). These previous studies suggest that sex, handedness, and behavioral asymmetry may each relate to callosal anatomy. In the present study, we consider the possibility

that groups differing in sex and handedness differ not only in callosal size, but in the relationship between callosal anatomy and behavioral asymmetry. We investigated both group differences in callosal size and group differences in the relationship between callosal size and behavioral asymmetry in a large sample of college students. Increased understanding of the relationship between callosal morphology and behavioral asymmetry may shed light on the role of the callosum in the coordination of interhemispheric interaction. Knowledge of how these relationships differ between groups defined by sex and handedness will contribute to our understanding of individual differences in brain/behavior relationships.

There have been many reports of sex differences in shape and proportional size of the corpus callosum (Suganthi et al., 2003; Sullivan, Rosenbloom, Desmond, & Pfefferbaum, 2001; Witelson, 1989). These studies have found that proportional callosal area (corpus callosum area/brain size) is larger in women. When brain size is statistically controlled using other methods, including ANCOVA and regression, sex differences are less apparent (Bishop & Wahlsten, 1997). One explanation for this discrepancy is that apparent sex differences in callosal anatomy may reflect sex differences in brain size (Bishop & Wahlsten, 1997; Luders et al., 2003). It is possible that individuals with smaller brains, regardless of their sex, have proportionately larger callosa (Jancke, Staiger, Schlaug, Huang, & Steinmetz, 1997; Leonard et al., 2008). In this framework, because

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women tend to have smaller brains than men, sex differences in callosal anatomy are explained by sex differences in brain volume. It has been demonstrated in the present sample that when effects of brain size are statistically controlled, the sexes do not differ in callosal size (Leonard et al., 2008).

Differences in callosal anatomy have also been reported between handedness groups. Several previous studies have compared callosal area between left-handed (LH) or ambidextrous subjects and right-handed (RH) subjects. The results of these studies have been mixed, with some groups finding no significant effects of handedness in mixed-sex groups (Hopper, Patel, Cann, Wilcox, & Schaeffer, 1994), some finding larger callosa in right-handers in a mixed-sex sample (Westerhausen et al., 2004), and some finding larger callosa in left-handed males than right-handed males (Tuncer, Hatipoglu, & Ozates, 2005). The inconsistency of these results suggests that the relationship between handedness and callosal anatomy is weak or nonexistent.

An alternate view of handedness is that the degree, rather than the direction, of handedness is the important dimension of variation. In this view, less strongly expressed handedness may be a marker of less strongly expressed functional lateralization in general. Participants with very strong hand preference, regardless of the direction of that preference, may differ from participants with less strong preference in how processing is distributed across the hemispheres (Christman, Propper, & Dion, 2004). Several studies demonstrate that individuals with a strong hand preference (consistent-handers) differ from other individuals (mixed-handers) on a variety of behavioral measures, including local–global processing (Christman, 2001), magical ideation (Barnett & Corballis, 2002), understanding of self-reference (Niebauer & Garvey, 2004), and episodic memory (Propper, Christman, & Phaneuf, 2005). Consistent-handers (CH) and mixed-handers (MH) also show differences in relationships between behavioral laterality and reading performance, with consistent-handers showing stronger asymmetry/performance relationships than mixed-handers (Chiarello et al., 2009b).

Christman argues that groups that differ in strength of hand preference display different degrees of interhemispheric interaction (Christman, 1993; Christman and Propper, 2001) and suggests that a larger corpus callosum in mixed-handers might support this greater interhemispheric interaction. One study demonstrated that male mixed-handers have larger total callosal area than male consistent-handers (Witelson & Goldsmith, 1991). Other studies have failed to replicate this handedness difference (Hines et al., 1992; Preuss et al., 2002). The present study affords the opportunity to investigate this question in a large sample composed of roughly equal numbers of CH and MH.

Main effects of sex and handedness on callosal anatomy may be tempered by interactions between sex and handedness. In a sample of 80 individuals (20 RH males, 20 RH females, 20 LH males, 20 LH females), females showed no significant effects of handedness on callosal area; while male LH had larger anterior and posterior bodies than male RH (Tuncer et al., 2005). Samples composed only of males demonstrate that non-consistent right-handers show larger areas than consistent right-handers (Denenberg, Kertesz, & Cowell, 1991; Witelson and Goldsmith, 1991), while a sample composed only of females showed no significant effects of handedness (Hines et al., 1992). The current study provided a sample of individuals within each sex and handedness group that was large enough to enable the use of multiple regression to investigate group differences in callosal anatomy.

Previous studies have investigated relationships between behavioral asymmetry and callosal area. Some such studies have failed to find relationships between callosal area and behavioral asymmetry, as measured by word reading (Kertesz, Polk, Howell, & Black, 1987) and patterns of activation in an fMRI word generation

task (Westerhausen et al., 2006a). Other studies examining relationships between behavioral lateralization and callosal anatomy have found negative correlations between asymmetry indices from dichotic listening tasks and area of all callosal subregions (Westerhausen et al., 2006b) or posterior callosal areas (Hines et al., 1992; Gootjes et al., 2006; Yazgan, Wexler, Kinsbourne, Peterson, & Leckman, 1995). Individuals with larger callosa have been shown to display a smaller leftward bias in line bisection and smaller leftward turning bias (Yazgan et al., 1995). These findings suggest that the callosum serves to facilitate the sharing of information between the hemispheres. In this framework, individuals with larger callosa would be expected to show a greater degree of communication between the hemispheres, and consequently reduced behavioral asymmetry.

In contrast, other studies demonstrate positive relationships between callosal area and behavioral lateralization. Males with larger callosa produced more errors in nonword trigram reading on left visual field/right hemisphere trials (Hellige, Taylor, Lesmes, & Peterson, 1998), as if the right hemisphere was functioning more independently. Lower left ear/right ear scores on a dichotic listening task were correlated with larger isthmus areas (Moffat et al., 1998). These findings suggest that another potential function of the callosum is to minimize interference between the hemispheres (Clarke, Lufkin, & Zaidel, 1993). In this framework, individuals with larger callosa would experience greater functional isolation of the hemispheres, and display larger hemisphere differences in performance.

One potential reason that studies may differ in the direction of relationship between behavioral lateralization and callosal area is that the corpus callosum may facilitate information transfer in some individuals or circumstances and inhibit information transfer in others. A larger corpus callosum, then, could be associated with stronger lateralization in some individuals or tasks and weaker lateralization in others.

Many of the previous studies investigating relationships between callosal morphology and language lateralization have included individuals of only one sex (Hines, 1992; Hellige et al., 1998; Westerhausen et al., 2006b) or only right-handed participants (Yazgan et al., 1995). Of the studies including individuals in each sex and handedness group, the maximum total number of participants was 104 (Kertesz et al., 1987), leaving small numbers of participants in each group. In the present study of 200 individuals, we explore the possibility that groups defined by sex and handedness differ in the relationship between lateralization of visual word recognition processes and callosal anatomy.

Previous studies have been limited in the behavioral tasks used to assess asymmetry. In the present study, we administered a variety of visual lexical tasks, ranging from basic word recognition tasks to tasks relying on semantic access. This allowed us to create a composite lexical asymmetry score, which served as a more general index of lexical lateralization as it is based on a variety of different tasks. Additionally, dichotic listening studies result in a measure of asymmetry only in accuracy of responses. The present study examined asymmetry in both reaction time and accuracy. The relatively moderate correlation between accuracy asymmetry and reaction time asymmetry in our sample (0.476) may indicate that these two variables represent partially independent metrics of behavioral asymmetry and should be considered separately.

In the present sample, we predict interactions between sex and consistency of handedness in callosal area, particularly in the anterior and posterior body and isthmus, subregions in which this effect has been previously seen when handedness was classified by direction (left-handedness versus right-handedness) (Tuncer et al., 2005). Under the assumption that larger callosal area supports greater interhemispheric communication, we predict that behavioral asymmetry and callosum area will be negatively correlated—individuals with the larger callosa are predicted to

show less difference between left and right-visual field performance. However, we investigated the possibility that groups defined by sex and handedness would show different relationships between callosal anatomy and behavioral asymmetry. Such a result might indicate that lateralization of word recognition processes is differentially related to callosal morphology across sex and handedness groups.

2. Methods

2.1. Participants

A total of 200 university students (100 females) were tested in the Biological Substrates for Language Project (Chiarello et al., 2006). Participants received \$100 payment for their participation. All were native speakers of English with normal or corrected-to-normal vision and ranged in age between 18 and 34 (mean age = 21.6). Their MRI scans were reviewed for neuropathology by a neuroradiologist (R.O.) and none had a history of neurological injury or illness.

2.2. Procedure

In a 2 h preliminary session, participants completed a 5-item hand preference questionnaire (Bryden, 1982), a pegboard measure of hand performance (Annett, 1985), questionnaires regarding language and family background, and standardized measures of reading skill and intelligence. Parental education was assessed on a scale ranging from 1 ("some high school") to 5 ("post-graduate or professional degree"). The word identification, word attack, and passage comprehension subjects of the WRMT-R/NU (Woodcock, 1998) were administered to assess participants' ability to read words, pseudowords, and to supply contextually appropriate completions to stimuli of increasing complexity. Percentile ranks from each subtest were used in analyses. Verbal and performance ability were assessed using the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999) and scaled scores were used in all analyses. Following this session, four test sessions were held on separate days in which participants completed seven lateralized word recognition tasks. After the final DVF task, participants completed the Adult Reading History Questionnaire (ARHQ) (Lefly & Pennington, 2000), designed to indicate a childhood history of reading disability. Higher scores on this measure indicate increasing likelihood of a childhood history of reading disability, with a score over 0.400 considered indicative of a childhood history of reading disability by the authors (Lefly & Pennington, 2000).

The hand preference questionnaire, made up of the five most reliable and valid items from the Edinburgh inventory (Bryden, 1982), was used to assess individuals' handedness. Scores on this index range from -1.0 (exclusive use of the left hand for all items) to 1.0 (exclusive use of the right hand for all items). Following Christman's method of dividing the sample into CH and MH (Christman et al., 2004), the groups were defined using a median split. The median handedness score for our sample was $+0.90$. Therefore, this served as the boundary for the MH group.¹ Participants with scores of 1.0 and -1.0 were classified as CH ($n = 103$). Five participants were strongly left-handed (score of -1.0). As the exclusion of these five individuals did not alter any of the results, we report findings for the entire sample, with these individuals coded as CH. Participants with scores between -0.9 and 0.9 were classified as MH ($n = 97$). The MH group therefore included participants who reported any use of the non-dominant hand, even if they preferred the dominant hand for most activities. MH had a mean handedness score of 0.49 , and 78% reported writing with their right hand. Thus, it should be noted that most mixed-handers had some degree of right-hand preference. Our sample included 28 non-right handers with handedness scores less than 0.4 (15 males), including five consistent-left-handers. Eleven of these individuals (5 males) had scores between -0.3 and $+0.3$, indicating very weak hand preference.

2.2.1. Divided visual field tasks

Stimuli for all DVF experiments consisted of 3–6 letter concrete nouns or pronounceable pseudowords. 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). Within each task, items were matched across visual field conditions on the basis of length, log frequency (Lund & Burgess, 1996), familiarity and imageability (Wilson, 1988).

¹ Because our modified handedness questionnaire consists of fewer items (5) than the 10-item Edinburgh Handedness Inventory used by Christman and colleagues, there is a higher probability of receiving extreme scores (either $+1.0$ or -1.0). Accordingly, our criterion for CH was higher than that reported by Christman in previous studies (Christman et al., 2004; Christman, Jasper, Sontam, & Cooil, 2007). Despite this apparent discrepancy, Christman has commented that "it seems to me that you did end up using the same median split that we use" (Christman, personal communication, November 11, 2008).

All stimuli were presented in uppercase, black 20 point Helvetica font on a white background. Macintosh computers were used for stimulus presentation and recording of manual responses in the visual field tasks. Pyscope 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 stabilize head position. For those experiments requiring manual responses, participants used their index fingers on the 'i' and 'x' keys to indicate one response and the middle fingers on the 'j' 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 analyzed.

Each DVF task began with practice trials, followed by the experimental trials. Subjects were instructed that the experiments investigated their ability to recognize words they were not directly looking at. They were told to maintain fixation on the central '+' fixation marker whenever it appeared on the screen, and to respond as quickly and accurately as possible. On each trial, the fixation marker appeared for 600–805 ms and flickered just prior to the onset of the stimulus. The stimulus word appeared randomly in the LVF or RVF. The innermost edge of the stimulus was 1.8° eccentric from the fixation marker. In order to prevent foveation of the stimuli, the duration of stimulus presentation was brief, ranging from 30 to 155 ms. The seven experimental tasks are described below:

- Pseudoword naming* Participants viewed pseudowords and pronounced them.
- Lexical decision* Participants viewed letter strings and indicated with a keypress whether each item was a word or a pseudoword. Half of the items were words and half were pronounceable pseudowords.
- Word naming* Participants viewed words and pronounced each.
- Masked word recognition* Participants viewed a word presented for 30 ms immediately preceded and followed by a pattern mask (@#@@) presented for 60 ms. Two words, differing by one letter, then appeared in the center of the screen, one above the other, and participants indicated by keypress the one which had been shown in between the symbols.
- Category generation* Participants viewed category names (e.g. FRUIT) and named a member of that category (e.g. APPLE).
- Verb generation* Participants viewed nouns (e.g. SCISSORS) and said a verb associated with the noun (e.g. CUT). Participants were instructed to respond with "what the object does or what it can be used for".
- Semantic decision* Participants viewed nouns and indicated by keypress whether each word represented something naturally occurring or manmade.

An overall RVF/left hemisphere advantage is routinely obtained in verbal tasks (Chiarello, 1988). With the exception of pseudoword naming RT, each task in the current study yielded group-level RVF advantages in both accuracy and RT (Chiarello et al., 2009a).

Composite measures will be more reliable than any single assessment (Rosenthal, 2005). To assess individual differences in overall speed and accuracy, composite average lexical performance scores (composite average accuracy and composite average RT) were computed for each participant by averaging LVF and RVF performance, z-scoring this average performance measure for each task, and then averaging across the seven tasks separately for percent correct and RT (see Chiarello et al., 2004 for a similar measure). Following a similar procedure, composite difference scores (composite accuracy difference and composite RT difference) for each task were calculated by subtracting LVF performance from RVF performance for each task, z-scoring this difference for each task, and then averaging across the seven tasks.

2.3. Image processing and neuroanatomical measurements

The images were reviewed for neuropathology by a neuroradiologist (R.O.) and then transferred to compact discs at the Imaging Center and sent to the McKnight Brain Institute at the University of Florida. Anatomical measurements were conducted blind to the behavioral analyses and vice versa. 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.

Gray, white and cerebrospinal fluid (CSF) volumes of each cerebral 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. This inter-rater reliability of this measure is $>.98$ (intraclass correlation). Total cerebral volume was calculated as the sum of the gray, white and CSF volumes.

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 (Witelson, 1989). One consistent-handed male and one mixed-handed male were identified as outliers because their callosal areas were 5.0 and 3.4 standard deviations larger than the mean, respectively. One consistent-handed female was identified as an outlier because her callosum was 2.4 standard deviations smaller than the mean. Even after careful inspection of the images for artefacts and repeated remeasuring by different operators, these individuals remained as outliers and were excluded from further analysis.

2.4. Measures

There are well-known relationships between overall cerebral volume and the area of the corpus callosum and a variety of techniques have been used to generate a measure of callosum size free from the effects of overall cerebral volume (Smith, 2005). Here, we report *residualized callosal area*, in which effects of cerebral volume are statistically controlled through regression. We chose to use residualized callosal area, rather than proportional callosum size, to eliminate effects of cerebral volume. This technique eliminates the variance in callosal area that is due to brain size. Group differences in this residualized measure, then, do not reflect group differences in cerebral volume. Residualized callosal area will be positive when the callosum is larger than would be predicted from cerebral volume alone and negative when the callosum is smaller than would be predicted from cerebral volume alone.

Similarly, individual differences in average RT and accuracy relate to the degree of VF difference that can be displayed—individuals who respond more quickly and accurately will necessarily show smaller raw differences between RVF and LVF performance. In order to investigate individual differences in asymmetry free from effects of average performance, we calculated residualized visual field difference scores from which average performance was partialled out. Using multiple regression, the visual field difference in accuracy or RT (*composite accuracy difference* and *composite RT difference*) is predicted from the average RT or accuracy (*composite average accuracy* and *composite average RT*) and the residual is stored for later analysis. This residualized difference score (*composite accuracy asymmetry* and *composite RT asymmetry*) reflects the degree to which an individual shows greater (positive residuals) or lesser (negative residuals) asymmetry than would be predicted based on their average performance. One consistent-handed female was identified as an outlier because her accuracy asymmetry score was 2.8 standard deviations larger than the mean. This individual was excluded from further analysis.

3. Results

3.1. Effects of sex and handedness

In order to examine whether groups differing in sex and consistency of handedness differ in age, level of parental education, verbal and performance IQ, percentile ranks on the reading subtests, scores on the ARHQ, composite average accuracy and composite average RT, composite accuracy asymmetry and composite RT asymmetry, total cerebral volume, or residualized callosal area, 2×2 analyses of variance (ANOVAs) were conducted with sex and consistency of handedness as variables. Group means for these measures are presented in Table 1. The groups defined by sex and consistency of handedness generally did not differ on demographic or psychometric measures. However, MH had significantly higher verbal IQ scores (110.5) than CH (107.2). Males had significantly higher percentile ranks on the word identification subtest (52.8) than females (46.0).

Groups defined by sex and consistency of handedness did not differ in composite average accuracy or RT from the DVF tasks. They also did not differ in accuracy asymmetry. However, there was a significant interaction of sex and consistency of handedness in RT asymmetry. Male CH show greater RVF advantages than male MH $t(96) = 2.12, p < .05$, Cohen's $d = 0.45$ while female CH and female MH do not differ $t(96) = 1.08, p > .10, d = 0.06$.

A prior report based on this dataset found that when corpus callosum area was expressed as a proportion of cerebral volume, females had relatively larger callosa (Leonard et al., 2008), but this effect was entirely due to variation in cerebral volume. In other words, individuals with smaller brains, regardless of sex, showed greater proportionate corpus callosum area. In this study, residualized callosal area was examined. This measure, unlike

the proportion measure, statistically controls for cerebral volume. When residual callosal size was examined, neither sex nor consistency of handedness was a significant predictor of total callosal area (see Table 1).²

In order to investigate interactions of sex and handedness in specific subregions of the corpus callosum, residualized area of each callosal subregion was calculated by statistically controlling for effects of cerebral volume through regression. These analyses revealed significant sex-by-handedness interactions in the rostrum $F(1,192) = 5.83, p < .05, \eta^2 = 0.029$ and the posterior body $F(1,192) = 4.46, p < .05, \eta^2 = 0.023$. Female CH have larger residualized rostrum areas (.015) than female MH (−0.012) $t(96) = 2.39, p < 0.05, d = 0.478$. Male CH and male MH do not significantly differ in residualized rostrum area (−0.013 versus .001), $t(96) < 1.2, d = 0.217$. Male CH show a trend toward smaller residualized posterior body areas (−0.027) than male MH (0.014), $t(96) = 1.78, p < .10, d = 0.359$. Female CH and MH do not significantly differ in residualized posterior body area (.005 versus −0.021), $t(96) < 1.2, d = 0.236$. Given the large number of comparisons made between the groups, and the borderline significance of these group differences, these effects should be interpreted with caution.

As a whole, these results suggest that groups defined by participants' sex and consistency of handedness are largely similar in terms of their performance on psychometric measures and experimental DVF tasks. The groups differ only minimally in residualized callosal area. With these findings in mind, we investigated whether the groups characterized by sex and consistency of handedness show different relationships between behavioral asymmetry and callosal area. Specifically, we examined whether similar sets of behavioral predictors were related to callosal size in each sex-handedness group.

3.2. Behavioral predictors of callosal area within sex and handedness groups

Within each sex-handedness group, a hierarchical multiple regression was carried out in which the area of the callosum was predicted from sets of related measures. In the first step, cerebral volume was entered. In the second step, performance and verbal IQ scores were entered in order to investigate whether individual differences in IQ account for variance in callosal size when cerebral volume is statistically controlled. In the third step, percentile ranks from the word identification, word attack, and passage comprehension subtests and scores on the ARHQ were entered in order to determine whether reading performance accounts for variance in callosal size above and beyond the effects of cerebral volume and IQ. In the fourth step, composite average accuracy and composite average RT were entered. In the final step visual field difference scores (composite accuracy difference and composite RT difference), were entered. Variance unique to the difference score, in this approach, indicates degree of behavioral lateralization free from the influence of brain size, IQ, reading skill, and overall performance. Results for each step of these regressions are presented in Table 2.

As expected, cerebral volume was a significant predictor of callosal area within each sex-handedness group. Once the variance attributable to brain size was accounted for, IQ scores, reading performance, and average task accuracy and RT did not significantly predict callosal area in any subgroup. However, after variance due to cerebral volume, psychometric measures, and average performance were accounted for, asymmetry of performance did predict callosal area in CH males and MH females.

² Similar results hold when proportional callosal area was compared between groups. There were no significant effects of sex or consistency of handedness on proportional callosal area (callosal area/cerebral volume⁶⁶⁶⁷), $F_s < 1$.

Table 1

Mean scores on psychometric tests, experimental tasks, and brain measures within sex and handedness groups.

Behavioral measures	Male CH	Male MH	Female CH	Female MH
N	43	55	57	41
Handedness questionnaire*	0.9	0.5	0.9	0.5
Age	21.9	21.6	21.5	21.4
Parental education	3.4	3.4	3.2	3.3
Verbal IQ**	106.7	110.5	107.5	110.6
Performance IQ	108.1	112.2	107.4	107.0
Word identification (percentile rank)***	53.2	52.5	44.6	48.0
Word attack (percentile rank)	52.9	48.7	44.3	46.1
Passage comprehension (percentile rank)	67.2	68.7	61.2	65.2
ARHQ	0.30	0.31	0.30	0.28
Composite average accuracy	−0.07	0.15	−0.08	0.01
Composite average RT	0.12	−0.03	−0.02	−0.04
Composite accuracy asymmetry	0.14	−0.03	−0.07	−0.03
Composite RT asymmetry****	0.13	−0.07	−0.06	0.04
Cerebral volume*****	1352	1323	1156	1192
Residual total callosum area	−0.173	−0.040	0.059	−0.050

* Significant main effect of handedness: $F(1,192) = 31.08$, $p < .0001$, $h^2 = .139$.** Significant main effect of handedness: $F(1, 192) = 4.71$, $p < 0.05$, $h^2 = .024$.*** Significant main effect of sex: $F(1, 192) = 7.64$, $p < 0.01$, $h^2 = .034$.**** Significant sex-by-handedness interaction: $F(1,192) = 5.32$, $p < 0.05$, $h^2 = .027$.***** Significant main effect of sex: $F(1, 192) = 101.95$, $p < .0001$, $h^2 = .338$.**Table 2**

Hierarchical multiple regression analysis of the contribution of cerebral volume, IQ (verbal and performance), reading measures (word identification, word attack, passage comprehension, and ARHQ), composite task averages (composite average accuracy and composite average RT), and composite task visual field differences (composite accuracy difference and composite RT difference) to total callosum area conducted separately for each sex and handedness group.

STEP	CH males		MH males		CH females		MH females	
	ΔR^2	$p <$	ΔR^2	$p <$	ΔR^2	p	ΔR^2	p
CV	.420	.001	.130	.010	0.258	0.001	0.199	0.005
IQ	.084	NS	.025	NS	0.017	NS	0.012	NS
Reading	.059	NS	.029	NS	0.084	NS	0.095	NS
Composite average	.002	NS	.034	NS	0.002	NS	0.096	NS
Composite difference	.124	.010	.062	NS	0.024	NS	0.214	0.005

The significance values are indicated in the “ $p <$ ” column.

To determine the individual contributions of accuracy and RT asymmetry to callosum area and the direction of these effects, the regression analyses were repeated with RT and accuracy asymmetry entered separately. The results of the last step of these analyses, in which the asymmetry scores for each DV were entered after variance accounted for by cerebral volume, psychometric measures, and average performance has been partialled out, are presented in Table 3 and Fig. 1.

Among CH males, accuracy difference scores were not significantly related to callosal area (Fig. 1, upper left panel); callosal area was significantly *negatively* related to composite RT difference scores, with smaller right-visual field advantages predicting larger area (Fig. 1, upper right panel). Among MH males, accuracy differ-

ence scores were not significantly related to callosal area (Fig. 1, middle left panel); there was a trend toward a negative relationship between RT difference scores and callosal area (Fig. 1, middle right panel). Among CH females, callosal area was not significantly related to composite accuracy difference scores (Fig. 1, middle panels). Among MH females, total callosum area was *positively* related to composite accuracy difference scores, with larger right-visual field advantages predicting larger area (Fig. 1, lower left panel); RT difference scores were not significantly related to callosal area (Fig. 1, lower right panel).³ These results are summarized in Table 4.

In order to examine whether relationships between callosal area and behavioral asymmetry differ for callosal subregions, we predicted area of each callosal subregion separately following the same hierarchical procedure that was employed in the prediction the area of the entire callosum. Because the step in which both RT and accuracy differences were entered was the only step which significantly improved the prediction of total callosum area, we focus on the relationships between the area of each callosal subregion and these composite difference scores, which are presented in Table 5. It should be acknowledged that we made no corrections for multiple comparisons, and many of the reported relationships are on the border of statistical significance. Therefore, these results should be considered with caution and future studies will be needed to validate these findings.

In CH males, composite asymmetry scores were significantly predictive of area of the middle body, isthmus, and splenium, with a trend toward significance in the genu. In MH males and CH females, there was no significant relationship between asymmetry and the size of any callosal subregion. In MH females, composite asymmetry scores were significantly predictive of area of the genu, anterior body, middle body, posterior body, and isthmus, with a trend toward significance in the rostrum as well. The relationship between asym-

Table 3

Significant predictors of total callosum area in each sex and handedness group.

Group	Predictors	Std. beta	T	$p <$
CH males	Composite accuracy difference	−0.17	0.86	NS
	Composite RT difference	−0.39	2.93	.010
MH males	Composite accuracy difference	0.07	0.36	NS
	Composite RT difference	−0.29	1.88	.100
CH females	Composite accuracy difference	−0.20	1.04	NS
	Composite RT difference	0.23	1.28	NS
MH females	Composite accuracy difference	0.77	4.00	.001
	Composite RT difference	−0.24	1.65	NS

³ Similar results hold for correlations between proportional callosum area and composite difference scores. Among CH males, the correlation between proportional callosum area and composite PC difference was not significant, $R < 0.20$, and the correlation with composite RT difference approached significance, $R = 0.25$, $p = 0.10$. Among MH males and CH females, neither difference score was significantly correlated with proportional callosum area, $R < 0.20$. Among MH females, the correlation between proportional callosum area and composite PC difference was significant, $R = 0.39$, $p < 0.05$, and the correlation with composite RT difference was not significant, $R < 0.20$.

Fig. 1. Relationships between corpus callosum area and behavioral asymmetry in groups defined by sex and consistency of handedness.

metry and area in CH males was strongest in the splenium, while in MH females the strongest relationships were observed in the genu. However, in both CH males and MH females, relationships between behavioral asymmetry and callosal area are distributed across the callosum.

4. Discussion

In this study, we set out to investigate whether groups defined by their sex and consistency of handedness differ in area of the corpus callosum or relationship between callosal area and lateralization of word reading. Before discussing our findings, we discuss some limitations of the study. We investigated lateralization only in

word reading and it is unclear whether similar relationships would be observed for other types of language tasks or other lateralized behaviors. Callosum size, additionally, is a rather gross and inaccurate measure of connectivity between the hemispheres. Findings that the midsagittal area of the corpus callosum is not significantly correlated with callosal fiber density (Aboitiz, Scheibel, Fisher, & Zaidel, 1992) or number of axons (Lamantia & Rakic, 1990) complicate interpretations of callosal area. Further studies investigating similar issues using more direct measures of connectivity, including diffusion tensor imaging, are necessary to more fully investigate relationships between behavioral laterality and morphology of the corpus callosum. Finally, the sample, while large, was restricted to college students, and it is difficult to know whether the results

Table 4
Summary of relationships between asymmetry and callosal area.

	CH males	MH males	CH females	MH females
Composite accuracy asymmetry	No relationship	No relationship	No relationship	Larger corpus callosum with larger RVF advantage
Composite RT asymmetry	Larger corpus callosum with smaller RVF advantage	No relationship	No relationship	No relationship

Table 5

Hierarchical multiple regression analysis of the contribution to the prediction of each callosal subregion of the composite difference step (in which composite accuracy difference and composite RT difference are entered together), after variance due to cerebral volume, IQ, reading measures, and composite task averages has been partialled out, for each sex and handedness group. Significant predictors are in bold and trends in italics.

	CH males		MH males		CH females		MH females	
	ΔR^2	<i>p</i> <	ΔR^2	<i>p</i> <	ΔR^2	<i>p</i>	ΔR^2	<i>p</i>
Rostrum	.007	NS	.002	NS	.027	NS	.131	.100
Genu	.079	.100	.019	NS	.020	NS	.279	.001
Ant. body	.026	NS	.019	NS	.041	NS	.163	.050
Mid body	.130	.050	.063	NS	.004	NS	.130	.050
Post. body	.028	NS	.105	.100	.015	NS	.175	.005
Isthmus	.110	.050	.022	NS	.048	NS	.126	.050
Splenium	.194	.005	.067	NS	.027	NS	.052	NS

generalize to a wider population. However, the large sample size and the variety of lexical tasks administered in this study allow us to contribute to a growing literature relating callosal anatomy to behavioral lateralization. It is worthy of note that in this sample, callosal morphology was not related to performance on psychometric measures or measures of non-lateralized performance. Instead, we demonstrate relationships between callosal area and lateralization of word recognition processes.

We obtained limited evidence that the sex and handedness groups in this sample differ in the lateralization of the visual word recognition processes investigated. Based on the hypothesis that group differences in callosal anatomy relate to group differences in behavioral lateralization, then, we predicted that the groups would not differ in the area of the callosum. Consistent with this prediction, when effects of brain size are controlled through multiple regression, males and females do not differ in callosal area, nor do groups defined by the consistency of their handedness. The lack of a handedness effect does not support Christman's suggestion that greater interhemispheric interaction in MH is associated with increased corpus callosum size (Christman, 1993; Christman and Propper, 2001).

Though the groups did not differ in accuracy asymmetry, there was a significant interaction of sex and consistency of handedness for RT asymmetry. Significant interactions of sex and handedness were obtained in the rostrum and posterior body. In the rostrum, female CH had larger areas than female MH while the males did not show reliable effects of handedness; in the posterior body, male MH had larger areas than male CH while females did not show reliable effects of handedness. This latter effect is consistent with a previous finding that the posterior body is larger in left-handed males than right-handed males (Tuncer et al., 2005). In this context, it is intriguing that MH males, but not females, show a trend toward smaller RT lateralization. It is possible that the larger posterior body area in the group of MH males, relative to the other sex and handedness groups, supports more interhemispheric communication and results in less lateralization of word reading processes.

Although group differences in both lateralization of word recognition processes and callosal size are limited, the relationships between these factors differ between the sex and handedness groups. Among CH males, callosal area was negatively related to behavioral laterality (smaller RT asymmetry scores predict larger area). MH males show weaker effects, in which smaller RT asymmetry scores predict larger callosal area at a trend level. Among CH females, no significant relationships between callosal size and behavioral laterality were observed. For MH females, behavioral asymmetry was positively related to callosal area (larger accuracy asymmetry scores predict larger callosal area).

The groups can be viewed as forming a spectrum with CH males and MH females at opposite ends. CH males show only negative associations between behavioral asymmetry and callosal area, while MH females show robust positive associations. MH males and CH females fall between these extremes, showing weak or absent

relationships between lateralization of word recognition and callosal area. In this light, it is interesting to note that collapsing over either sex or handedness would dilute group effects by combining a group that shows effects with a group that does not. This could explain some inconsistency of results of prior studies examining only sex or handedness differences in callosal size.

The relationship between behavioral laterality and callosal anatomy is most robust for the MH females. This negative relationship is strongest in the genu, though other subregions of the callosum also show significant relationships. This region of the callosum exhibits a higher proportion of thinner, slower-conducting fibers and supports hemispheric interaction between association areas (Aboitiz et al., 1992). It is possible that behavioral lateralization in MH females is more strongly associated with higher order processing that takes place in the regions linked by this portion of the callosum. The negative correlations for this group may suggest inhibitory interactions (Thiel et al., 2006; Westerhausen et al., 2006b). CH males display positive relationships between lateralization of word recognition processes and callosal area that are more spatially limited, restricted to posterior regions of the callosum. These posterior regions exhibit a higher proportion of large diameter fibers, thought to have higher conduction velocity and support information transfer between the hemispheres (Aboitiz et al., 1992). It is possible that the behavioral laterality of CH males is more strongly linked to the interhemispheric transfer of sensory information. MH males and CH females show no reliable relationships between lateralization of word recognition tasks and callosal size.

Group differences in the relationship between callosal area and behavioral asymmetry may relate to differences in callosal microstructure. At a cellular level, callosal transmission has been shown to have both excitatory and inhibitory effects (Conti & Manzoni, 1994; Innocenti, 2008; Kawaguchi, 1992). Group differences in the balance of excitatory and inhibitory transmission might result in different relationships between callosal size and behavioral lateralization. Diffusion tensor imaging has revealed effects of sex and handedness on measures of molecular diffusion (Westerhausen et al., 2003, 2004). Thus, it is possible that group differences in fiber composition result in different functional consequences of callosal morphology between sex and handedness groups, differences that are not revealed by corpus callosum area measurements.

These group differences in relationships between asymmetry of word recognition and morphology of the callosum may reflect group differences in how the hemispheres interact. The CH males in this study show relationships similar to those seen in the majority of dichotic listening studies (smaller asymmetry scores with larger callosal area) (Hines, 1992; Gootjes et al., 2006; Westerhausen et al., 2006b; Yazgan et al., 1995). In this group, it is possible that larger callosa support greater interaction between the hemispheres and allow more equivalent performance between the two visual fields. The MH females show a relationship opposite those most

commonly seen between asymmetry of dichotic listening and callosal anatomy (larger asymmetry scores with larger callosal area). It is possible that, within this group, a larger callosum serves to minimize interference between the hemispheres.

Overall, the results of our study suggest that no simple and universal relationship exists between behavioral asymmetry and anatomy of the corpus callosum. Instead, relationships between behavioral lateralization and callosal anatomy may be moderated by sex and handedness. In order to observe robust associations between the area of the corpus callosum and lateralization of word recognition processes, it may be necessary to examine relationships within sub-populations. Our study demonstrates the importance of considering brain/behavior relationships within groups defined by sex and consistency of handedness.

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