

Relationship between intelligence and the size and composition of the corpus callosum

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Abstract We investigated the relationship between the morphology of the corpus callosum (CC) and IQ in a healthy sample of individuals in their late teens and early twenties. The relationship between the area of the CC, measured at the midline, and IQ showed regional differences. We observed that a higher estimated performance IQ was associated with smaller area in the posterior regions of the CC, a finding that differs from a positive association previously observed in a somewhat older adult sample. In contrast, higher estimated verbal IQ was associated with decreased fractional anisotropy of the genu, an anterior portion of the CC. Age effects were also observed such that older age was associated with larger CC area. Our results suggest that CC morphology is related to cognitive performance, which may have implications for clinical populations in whom CC morphology is atypical.

Keywords Corpus callosum · Intelligence · Age · Gender differences · DTI

Preface

In this paper we examine the relationship between intelligence, as measured by a brief IQ test, and the morphology of the corpus callosum (CC), which connects homologous areas of the left and right hemispheres of the brain and is the largest fiber tract in the human brain (Hynd et al. 1991; Hoptman and Davidson 1994; Banich 2003; Innocenti and Bressoud 2003). An examination of the structure of the CC and its relationship to behavior is particularly apt for this special issue in honor of Prof Giovanni Berlucchi, who has been a pioneer in describing the functions of the CC. In his early work, Prof. Berlucchi conducted ground-breaking research that characterized the function of the CC in cats (Berlucchi 1965, 1966) and demonstrated its importance in binding together two halves of the visual world (Berlucchi and Rizzolatti 1968). He eloquently reviewed how the anatomy and physiology of the CC supports visual function (Berlucchi 1972) and has shown how interhemispheric integration influences the processing of information in other brain regions, such as the superior colliculus (Antonini et al. 1979). This work was extended by looking at the larger role of the CC in learning in cats (Berlucchi et al. 1979) and examining issues of interhemispheric transmission in humans (Tassinari et al. 1983). The implications of such transmission in humans have also been considered, such as in work noting that the visuo-motor transfer of information is the longest lasting sign of callosal disconnection after traumatic brain injury (Peru et al. 2003). Finally, with his keen appreciation for the history of science, he considered how the work of Roger Sperry on the CC and that of David Hubel and Torsten Wiesel on visual processing, all three of whom received the Nobel prize in 1981, fits into the tradition of neuroscientific research dating back to Cajal (Berlucchi 2006). We are honored to be

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able to contribute a paper to this special issue in honor of Prof. Berlucchi's retirement as his work has informed both this particular article and the larger program of research in the Banich laboratory for years.

Introduction

Research with split brain patients, who have had the CC severed for the treatment of epilepsy, and those with agenesis of the CC, where the CC does not develop fully or is completely absent, has indicated that the CC is crucial to the interhemispheric transfer of information (Sperry et al. 1969; Kreuter et al. 1972; Dimond 1976). In addition to binding together the two halves of the sensory world that are represented in opposite hemispheres, the CC also appears to play a role in attentional control (see Banich 2003, for a review). As initially described by Banich and Belger (1990), interaction between the hemispheres is beneficial to task performance under conditions of high attentional demand but is detrimental to performance under conditions of low demand. Based on a large body of empirical work (e.g., Banich and Belger 1990; Belger and Banich 1992, 1998; Weissman and Banich 1999, 2000), Banich and Brown (2000) argued that three factors determine whether interhemispheric interaction is beneficial or detrimental to task performance. One factor is the degree to which the callosal transfer of information increases the time required for processing information. A second factor is the extent to which a task's computational complexity taxes the processing resources of a single hemisphere. The third factor is the capacity of an individual's CC to transfer information between the hemispheres.

According to this model, it is generally beneficial for information to be processed by a single hemisphere when a task is computationally simple. Because the transfer of information between the hemispheres engenders a cost in time, it will be faster for a single hemisphere to perform the task when it has the capacity to do so. However, when tasks are more demanding, interhemispheric interaction leads to better task performance because the processing load can be divided between the hemispheres. Hence, the benefit of recruiting additional resources by using both hemispheres outweighs the time cost of CC transfer, making it advantageous compared to within-hemisphere processing (for a review, refer to Banich 1995, 1998, 2003; Banich and Brown 2000). However, atypical morphology of the CC, which can occur with multiple sclerosis (Pelletier et al. 2001), schizophrenia (Shenton et al. 2001), Alzheimer's disease (Wang et al. 2005), traumatic brain injury (Mathias et al. 2004), and attention deficit hyperactivity disorder (Valera et al. 2006; Hutchinson et al. 2008), may compromise the ability of the CC to effectively distribute the processing load. As a result, interhemispheric interaction may

be less advantageous in boosting task performance on complex tasks.

Given this model, one might expect a relationship between performance on cognitive tasks and CC structure. In fact, there is evidence supporting such a relationship between IQ and CC morphology in studies of clinical populations in which the CC is affected. For example, two patients with tumors located in the splenium of the CC have been found to have impaired performance IQ but relatively intact verbal IQ (Osawa et al. 2006). In another study, the area of the CC in males who were diagnosed with lacunar infarction (stroke) and white matter abnormalities was positively correlated with both performance and verbal IQ (Yamauchi et al. 1994). In addition, CC area was smaller in these patients. The authors concluded that intellectual decline is associated with atrophy of the CC after stroke.

A similar relationship has been observed in a number of developmental studies. Adolescents with mental retardation, and by definition low IQ, are more likely to show thinning of the CC (Spencer et al. 2005) and reduced white matter density in the posterior CC (Spencer et al. 2006). Other studies have found a relationship between CC size and IQ in children and adolescents who were born pre-term, such that a smaller CC was associated with a lower IQ (e.g., Peterson et al. 2000; Caldu et al. 2006; Allin et al. 2007; Narberhaus et al. 2007). Similarly, in individuals with epilepsy, a larger posterior CC area has been associated with higher IQ (Strauss et al. 1994). Therefore it is possible that IQ and CC morphology are related, particularly for posterior regions of the CC.

Notwithstanding these findings, the evidence for an association in neurologically intact individuals is generally equivocal. In a large sample of healthy individuals ranging in age from 6 to 88 years, a measure related to CC morphology (which was interpreted to represent a thinner and more concave anterior body of the CC) was associated with higher IQ, while conventional measures of CC size were not (Peterson et al. 2001). Similarly, other studies have failed to find a relationship between CC area and IQ, including a study by Nosarti et al. (2004) of neurologically intact 14- to 15-year olds and one by Tramo et al. (1998) who examined this issue in monozygotic twins. Moreover, two studies that used voxel-based morphometry to examine white/gray matter volume failed to find a significant relationship between white matter in the CC and intelligence (Haier et al. 2004, 2005).

In contrast, other studies have found a relationship between IQ and the CC in healthy individuals. In a twin study, Hulshoff Pol et al. (2006) examined which brain regions show a high degree of heritability and are related to IQ, a trait which is also known to be heritable (Plomin and Spinath 2004). They examined monozygotic and dizygotic twins and found that the structure of the CC was highly

heritable (0.82) and that CC white matter density shared a genetic origin with IQ, such that greater white matter density was correlated with higher IQ. However, they also found that environmental influences were associated with white matter density of the anterior CC, suggesting that not all portions of the CC have equal genetic influence.

Moreover, Luders et al. (2007) found significant positive correlations between IQ and the thickness of the CC across the posterior portion of the CC (posterior body, isthmus, anterior portion of the splenium) and across a portion of the anterior midbody in healthy adults. In their study, thickness was measured as the distance between points on the superior and inferior surfaces of the CC on the midsagittal section of the brain. Interestingly, these relationships were less pronounced for females. In contrast, Allin et al. (2007) observed that higher IQ was associated with a smaller posterior section of the CC in adolescents (mean age of 15) and adults (mean age of 22) who were controls for a sample of individuals born pre-term. In this latter study, the CC was divided into quarters (anterior, midanterior, midposterior, posterior). One possible explanation for the differences in the direction of the relationship between the CC and IQ reported by Luders et al. (2007) and Allin et al. (2007) is that the age of participants varied in these two studies. The CC continues to develop throughout adolescence and into early adulthood (Giedd et al. 1999; Thompson et al. 2000; Barnea-Goraly et al. 2005). As such, the relationship between CC size and IQ may vary depending on an individual's age.

Given these contradictory findings, the goal of the present study was to examine the relationship between CC area and IQ in a group of individuals aged 14–25. There were two main objectives. First, we wanted to determine whether the results of Allin et al. (2007), which showed a negative relationship between IQ and posterior CC area, could be replicated in a sample whose ages spanned the two ages (age 15, age 22) examined in their study. Second, we investigated the potential influence of age on CC area and its relation to IQ. In doing so, we explored whether the relationships between CC area and integrity differed for estimates of verbal IQ (VIQ_{est}) and performance IQ (PIQ_{est}), given that these aspects of intelligence have been found to be somewhat dissociable, and whether patterns differed for males and females given reports of gender differences in CC size (Bishop and Wahlsten 1997; Sullivan et al. 2001). This study should improve our understanding of CC development and its relationship to intellectual abilities.

Method

This study was approved by the Colorado Multiple Institutional Review Board and was conducted in accordance with the Helsinki Declaration.

Participants

Thirty-one males and 40 females from the general community, aged between 14 and 25 years (mean age = 19.2, SD = 3.3), participated in this study.

MRI acquisition and analyses

T-1 weighted 3D-SPGR anatomical images were collected on a 3 T GE-Signa MR scanner (repetition time = 9 ms, echo time = 2.012 ms, flip angle = 10°, inversion time = 500 ms; 220 mm field of view, 256 × 256 matrix, 0.8594 mm × 0.8594 mm in-plane resolution, 124 slices, 1.7-mm slice thickness). Slices were acquired coronally. These images were used to determine CC area. In addition, DTI images were obtained using single shot echo planar sequence of 25 gradient directions, each with a weighting of $b = 1,000 \text{ s/mm}^2$ and NEX = 2, along with one volume without diffusion weighting. The acquisition matrix was 128 × 128 and the images were zero-filled to 256 × 256 (repetition time = 10,000 ms, echo time = 85 ms, flip angle = 90°, 128 × 128 matrix, 1.09 mm × 1.09 mm in-plane resolution, 20 slices, 4 mm slice thickness).

IQ measurement

Participants completed the two subtest version of the Wechsler abbreviated scale of intelligence (WASI), consisting of the Matrix Reasoning and Vocabulary subtests (Wechsler 1999). Matrix Reasoning provides an estimate of performance IQ (PIQ_{est}) and Vocabulary provides an estimate of Verbal IQ (VIQ_{est}).

CC measurement

The midsagittal slice was defined as that slice in which the cerebral aqueduct could be observed most clearly. The CC in that slice was then traced and divided into five regions, using a semi-automated algorithm developed by BLJ. Hofer and Frahm's (2006) five subdivisions of the CC were utilized because they are based on the origins and projections of the fibers in the CC, as determined by tractography. These regions are defined by drawing a line between the most anterior and posterior points of the CC. Divisions are placed perpendicular to this line, at 1/6, 1/2, 2/3, and 3/4 of its length, thus dividing the CC into five regions. These subdivisions connect, from anterior to posterior (1) prefrontal regions, (2) premotor and supplementary motor regions, (3) primary motor cortices, (4) primary sensory cortices and (5) parietal, temporal, and occipital cortices.

Although one rater (ADH) conducted all of the CC measurements, intra-rater and inter-rater reliability of the CC measurements were assessed in a subset of 33 participants

from the current sample. Intra-rater reliability was assessed by having ADH redo the area measurements for these participants, while being blinded to the original scores. When these measurements were compared, total CC size had an inter-class correlation coefficient of 0.98 and reliability coefficients for the CC regions ranged from 0.95 for region 3 to 0.98 for regions 1, 2 and 5. Inter-rater reliability was calculated for the CC measurements of the first author (ADH) and the fifth author (ANB), yielding coefficients of 0.91 for total CC size and between 0.85 for region 4 and 0.95 for region 1 for CC regions. Thus, this method had very good intra-rater and inter-rater reliability.

Whole brain volume (WBV) was additionally calculated to control for differences in CC size that may be related to more general differences in brain size and volume. WBV was calculated using unnormalized volumes from SIENAX in FSL (Smith et al. 2002, 2004).

Diffusion tensor imaging

Diffusion tensor imaging (DTI) data, yielding a measure of fractional anisotropy (FA), was also obtained to examine the white matter integrity of the CC. FA is a measure of the diffusion of water molecules along the direction of the axon and provides a quantitative metric of white matter integrity. Our approach was to examine two regions that we believed would provide a representative measure of FA within the CC, one located in the genu and one in the splenium. This approach was exceedingly conservative in order to ensure that we were obtaining a measurement from CC tissue that was not influenced by partial volume effects, which would occur if a voxel contained both CC and surrounding tissue. Because our axial slice thickness was 4 mm, we restricted our analysis to FA in the thickest part of the genu and the splenium that contained voxels entirely within the CC.

To obtain FA measures in the genu and splenium, regions of interest (ROIs) that encompassed each of these regions separately were manually defined based on FA maps. Manual determination was required to define these areas due to the variation in size and shape of the CC across individuals and, as a result, the ROIs varied in size. These ROIs were square in-plane but varied in the number of slices that were included. When defining the ROI, the following constraints were applied. Where possible, the ROI was drawn to at least one or two voxels past the obvious border of the CC with non-callosal tissue, which could be easily determined because the FA in the CC is much higher than in the surrounding tissue. In the *y* direction, the ROI was drawn to end at regions in which the CC appeared significantly thinner and/or the FA values for a voxel suggested partial volume effects. In the *x* direction, boundaries were drawn to be centered on the midline of the CC. The sizes of the ROIs ranged from 3,174 to 28,717 voxels, with

an average of 8,896 voxels (SD = 4,442) for the genu and ranged from 2,304 to 8,060 voxels, with an average of 4,928 (SD = 1,188) for the splenium.

We then determined the number of voxels within this ROI that met a set of criteria suggesting that they indeed represented CC tissue. First, because CC fibers at the mid-sagittal slice are oriented along the *x* axis, the primary eigenvector could not deviate more than 11.48° from the *x* axis. Second, based on mean and SD of FA values from controls (mean age = 39) in a DTI study of CC morphology undertaken for other purposes (Rotarska-Jagiela et al. 2008), the voxel had to have an FA of at least 0.6 in order to ensure that the voxel was CC white matter. Although the sample in the Rotarska-Jagiela study was older than ours, it represents the values that would be observed in a “mature” CC. Finally, it was important that the voxels in the slices above and below the voxel in question had an FA value indicating that at least a portion of it contained white matter of the CC. Therefore, based on FA values from Rotarska-Jagiela et al. (2008), the third requirement was that the neighboring voxels had an FA of at least 0.35, which would indicate that at least part of the volume in that voxel represented white matter of the CC. The threshold for the neighboring voxels and the *x* component of the primary eigenvector were varied in a subsample of participants to ensure that our results were not driven by the choice of thresholds (Hutchinson et al. 2008, unpublished data). Only results for FA > 0.35 and $\alpha < 11.48^\circ$ are presented because variations in these parameters did not affect the results. The voxels identified by the algorithm were checked visually to confirm that they were located in the CC and that no voxels that were obviously part of the CC had been excluded by the algorithm and, consequently, were not contained in the ROI. One of our dependent measures was the number of voxels within the ROI that met the criteria for being mid-line CC tissue (i.e., FA > 0.6 and primary eigenvector could not deviate more than 11.48° from the *x* axis).

We also took a second approach to obtaining a representative index of peak FA within each ROI. The peak FA value within the ROI was determined and then a standard size slab (3 × 3 × 1 voxels in the *x*, *y* and *z* directions, respectively) was drawn around that peak. Hence, we obtained two measures for each ROI: one that provided an index of how many voxels were likely to meet our criteria for representing “mature” midline CC tissue, and one that provided an estimate of the peak FA value within the ROI.

Results

The CC measurements for this sample are presented in Table 1. The total CC area measurements observed were within the range of CC measurements observed in the

Table 1 Midsagittal CC area measurements using Hofer and Frahm's (2006) divisions

	Total CC (cm ²)	1	2	3	4	5	WBV × 10 ⁶ mm ³
Mean	6.29	1.59	1.82	0.85	0.40	2.36	1.20
SD	0.94	0.26	0.27	0.18	0.08	0.36	0.11

samples of healthy controls examined by other studies [5.10 cm² (Zanetti et al. 2007) to 6.51 cm² (Miyata et al. 2007)]. Therefore, the CC measurements in the current sample appear to be comparable to those in other studies.

Relationship between CC area and age

Our goal was to determine the specific relationship between age and CC area. WBV was associated with increased CC area ($r = 0.29$) and modestly associated with age ($r = -0.06$) in our sample. Thus, to determine whether there was any relationship between CC area and age that could not be accounted for by WBV, we calculated partial correlations controlling for WBV. There was a positive relationship between total CC area and age ($r = 0.28$, $P = 0.02$) (see Fig. 1). Interestingly, although regions 1, 2, 4 and 5 showed small to medium positive (albeit non-significant) correlations with age, region 3, which connects the primary motor cortices, was significantly negatively correlated with age. This correlation represents a moderate relationship (Cohen 1988) and remained significant after correcting for multiple comparisons. However, this relationship may be gender specific, as there was a negative correlation for females ($r = -0.51$, $P = 0.001$) but not for males ($r = 0.06$, $P = 0.78$). Moreover, this was the only significant correlation between area for any region of the CC and age for female participants. In contrast, the size of regions 1 ($r = 0.36$, $P = 0.05$) and 2 ($r = 0.39$, $P = 0.04$) were significantly correlated with age in males, as was total CC size ($r = 0.46$, $P = 0.01$), such that a larger CC was associated with older age in males. However, these correlations did not remain significant after Bonferroni corrections for multiple comparisons.

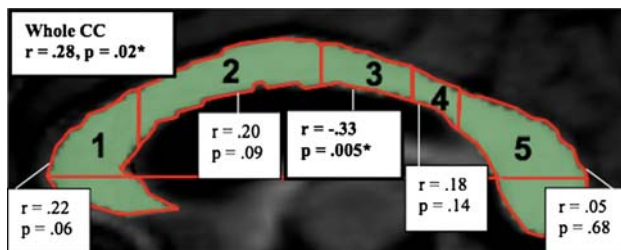


Fig. 1 Correlations between CC area and age, controlling for whole brain volume. * $P < 0.05$

Relationship between FA and age

Partial correlations were conducted between measures of FA, which serve to index CC integrity, and age with WBV entered as a covariate. There were no significant correlations between FA measures of CC integrity and age for the group as a whole. However, when males and females were considered separately, there was a significant positive correlation between the number of voxels that met the criteria in the genu and age for males ($r = 0.49$, $P = 0.008$), which remained significant after correcting for multiple comparisons.

Relationship between CC area and IQ

In our sample, estimated FSIQ (FSIQ_{est}) ranged from 79 to 140 with a mean of 106.9 (SD = 10.8). The Matrix Reasoning subtest scaled score (which was used as an estimate of performance IQ, PIQ_{est}) ranged from 6 to 17, with a mean of 11.9 (SD = 2.2) and the Vocabulary subtest scaled score (which was used as an estimate of Verbal IQ, VIQ_{est}) ranged from 3 to 19, with a mean of 10.8 (SD = 2.6).

The relationships between total CC area and IQ estimates were examined in three ways: (1) by simple bivariate correlations, (2) by partial correlations, controlling for WBV because WBV was modestly related to FSIQ_{est} ($r = 0.19$), PIQ_{est} ($r = 0.34$) and VIQ_{est} ($r = 0.05$), and (3) by correlations controlling for both WBV and age due to the relationship between CC area and age discussed above (see Table 2).

Because prior studies have noted a relationship with posterior sections of the CC, we initially focused on this region. To do so we divided the CC in half calculating the anterior half as the sum of areas 1 and 2, and the posterior half as the sum of areas 3, 4 and 5. This analysis revealed a significant negative correlation between FSIQ_{est} and the posterior half that passed Bonferroni correction both when WBV ($r = -0.25$) and when WBV and age ($r = -0.24$) were considered as covariates. No relationship was observed for the anterior half.

To examine the nature of this relationship in more detail, we investigated the relationship between PIQ_{est} and VIQ_{est} with each of the CC regions (areas 1–5). A negative correlation was observed for the simple bivariate correlation between the area of region 3 and PIQ_{est} ($r = -0.26$, $P = 0.031$). Although this correlation was not significant after Bonferroni corrections, it passed Bonferroni correction when WBV was entered as a covariate ($r = -0.37$, $P = 0.002$) (see Fig. 2). Negative correlations (that did not pass Bonferroni corrections) were also found between PIQ_{est} and the area of regions 4 and 5, possibly suggesting a larger relationship between PIQ_{est} and posterior regions of the CC. There were no significant correlations between VIQ_{est} and CC area.

Table 2 Correlations between PIQ and VIQ estimates and CC area and fractional anisotropy (FA) with no covariates, WBV alone, and WBV and age entered as covariates

	No covariates		Covariate: WBV		Covariate: WBV and age	
	PIQ	VIQ	PIQ	VIQ	PIQ	VIQ
CC area						
Total CC	0.01	-0.04	-0.10	-0.05	-0.21	-0.12
1	0.12	0.01	0.02	-0.01	-0.06	-0.06
2	0.00	-0.01	-0.11	-0.03	-0.19	-0.08
3	-0.26	-0.19	-0.37*	-0.20	-0.30	-0.15
4	-0.06	-0.03	-0.18	-0.05	-0.25	-0.09
5	-0.15	-0.13	-0.25	-0.15	-0.28	-0.16
CC FA						
Genu: # voxels	0.05	-0.27	-0.08	-0.30	-0.15	-0.35*
Genu: Mean FA	0.04	-0.24	-0.06	-0.26	-0.08	-0.27
Splenium: # voxels	-0.05	-0.01	-0.07	-0.01	-0.15	-0.05
Splenium: Mean FA	-0.07	0.09	-0.06	0.09	-0.04	0.11

WBV whole brain volume, CC corpus callosum, FA fractional anisotropy

Voxels represents the number of voxels in the ROI that met our criteria for being considered CC tissue; Mean FA represents the mean FA of the voxels so identified as callosal tissue

* Significant after Bonferroni corrections for multiple comparisons ($P < .05$)

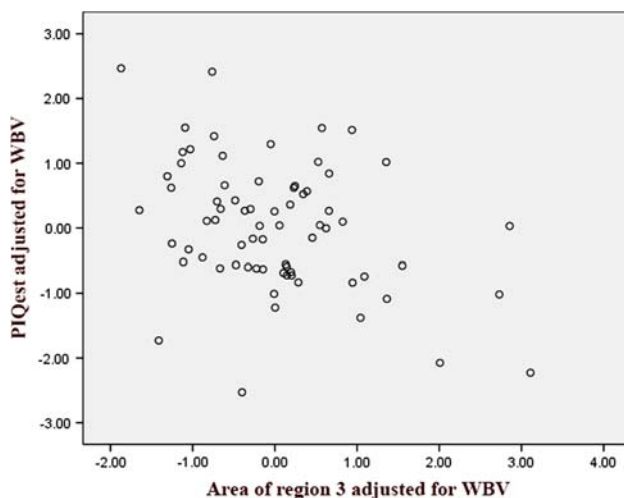


Fig. 2 The relationship between PIQ_{est} (adjusted for WBV and age) and the size of region 3 (adjusted for WBV and age)

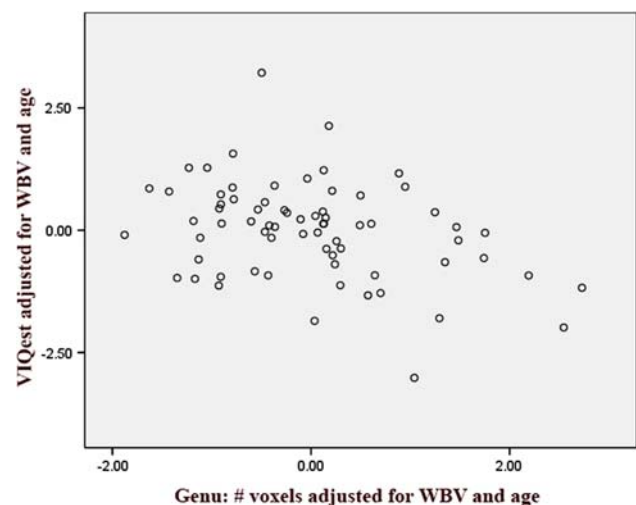


Fig. 3 The relationship between VIQ_{est} (adjusted for WBV and age) and FA (number of voxels) in the genu (adjusted for WBV and age)

When males and females were considered separately, none of the correlations remained significant after Bonferroni corrections for multiple comparisons, possibly due to reduced statistical power associated with the smaller group sizes.

Relationship between FA and IQ

The relationships between CC integrity, as indexed by our two FA measures, in the genu and splenium and estimates

of IQ were examined in the same manner as CC area (see Table 2). Lower VIQ_{est} was associated with increased integrity, as indexed by both measures of FA for the genu. These correlations were also present when controlling for WBV alone and both WBV and age. However, after corrections for multiple comparisons, the only effect that remained significant was the relationship with the number of voxels identified in the genu when controlling for both WBV and age (see Fig. 3). There were no significant correlations between PIQ_{est} and FA.

Discussion

The present study provides insight into some of the factors that are associated with CC morphology. Consistent with the findings of Allin et al. (2007), our data suggest that smaller areas in posterior regions of the CC are associated with higher intelligence. This effect was significant for region 3 with a trend for regions 4 and 5, and appears to be mediated by PIQ_{est} (rather than VIQ_{est}), an issue which we discuss in more detail below. In our study, participants' ages ranged from 14 to 25 with a mean age of 19, spanning the two developmental time points—ages 15 and 22—examined by Allin et al. (2007). Although our results and those of Allin et al. (2007) are in accord, they conflict with the findings of Luders et al. (2007) who reported that higher IQ was associated with a thicker posterior CC in healthy adults with a mean age of 28. Our study differed from that of Luders et al. (2007) who examined CC thickness, rather than CC area and integrity (as was done in the current study). However, this difference seems unlikely to account for the conflicting results, especially given that our results are consistent with those of Allin et al. (2007).

A more likely explanation for the difference in findings is that they arise from developmental factors. Although it had been traditionally thought that the CC reached maturity by early adolescence (Yakolev and Lecours 1967), more recent work suggests a maturational gradient that extends into young adulthood (Giedd et al. 1999; Thompson et al. 2000; Barnea-Goraly et al. 2005). We propose, based on prior work done in our laboratory (for a review refer to Banich 1995, 1998, 2003; Banich and Brown 2000) that during adolescence and early adulthood, the negative relationship between CC measures and IQ relates to the processing capacity of each hemisphere. By this account, when an individual has a high IQ, there is less need to recruit the other hemisphere to increase the computational power available to complete complex tasks than in lower IQ individuals. Therefore, if youth and young adults with a high IQ have had less need and therefore less experience in requiring interhemispheric interaction to meet task demands, their CC fibers may not have needed to become as myelinated as in less intelligent individuals.

There is precedent for the idea that individual differences in experience can affect the myelination of the CC. For example, adults who began musical training before the age of 7 have been reported to have a larger anterior half of the CC (Schlaug et al. 1995) and musicians display a significantly greater FA in the genu of the CC (Schmithorst and Wilke 2002). Moreover, individuals who are illiterate have been shown to have a thinner posterior midbody, which is thought to contain fibers connecting parietal regions that are involved in reading (Castro-Caldas et al. 1999). In a similar manner, less of a requirement to integrate informa-

tion between the hemispheres in adolescents and young adults with higher IQs may result in less myelination.

However, an explanation is also needed for the findings of Luders et al. (2007) who found that, in an older sample, a larger posterior CC area was associated with higher IQ. Considering that as one ages the repertoire of abilities to be performed becomes more demanding, our account would suggest that it is likely that within-hemisphere resources will become less able to meet task demands. Under such conditions, there will be an increased benefit from the recruitment of the other hemisphere through interhemispheric interaction. If individuals with a higher IQ can handle more cognitively demanding tasks, with time there may be a switch to increased reliance on interhemispheric interaction. The net result would be the relationship observed by Luders et al. (2007): a larger CC is associated with a higher IQ. This hypothesis could be effectively examined in future studies that take a longitudinal examination of the relationship between CC area and IQ during young adulthood.

We also found that integrity of white matter (as measured by FA) in the genu, but not the splenium, was related to IQ. More specifically increased FA in the genu, which connects prefrontal regions, was associated with lower VIQ_{est} . This finding demonstrates the value in examining both CC area and integrity because the relationship with different aspects of IQ (VIQ_{est} , PIQ_{est}) varied for these different measures. What is notable is the consistency in that both relationships with area and FA are negative, such that larger CC size or increased FA (which is thought to index myelination among other aspects of CC morphology), are each associated with decreased IQ, most likely for the reasons described above.

It is not clear in the present study why there is an association of PIQ_{est} with aspects of posterior CC morphology and an association of VIQ_{est} with aspects of anterior CC morphology. One possible explanation is that the processes tapped by each subtest used to provide estimates of VIQ and PIQ rely on different brain regions and hence show different relationships with regions of the CC. For example, the Matrix Reasoning subtest, requires spatial processing that relies on parieto-temporal areas of the brain, connected through more posterior regions of the CC. In contrast, the Vocabulary subtest may rely on temporal and more importantly frontal regions involved in language and semantic processing, which do send fibers through the splenium but may send some fibers through the genu. But as noted below, the different associations of VIQ_{est} and PIQ_{est} with CC morphology must be interpreted cautiously.

The limitations of our study should be considered as well. The current sample size is relatively modest and will need to be replicated with a larger sample. Furthermore, although our findings were consistent across CC regions and whether covariates were included or not, they did not always reach

significance when taking multiple corrections into account. Our FA measures were also restricted to the genu and the splenium preventing an examination the potential relationship between IQ and FA of the CC midbody. In addition, our estimates of IQ were not drawn from the WAIS but rather we used the two subtest version of the WASI, which is a short form of the WAIS intended for use in screening, research or reassessments (Axelrod 2002; Psychological Corporation 1999). Hence, our measure of FSIQ_{est}, VIQ_{est}, and PIQ_{est} provide a quick estimate of intellectual abilities. We should note that because of the limitations of the WASI, the fact that PIQ_{est} seemed to be a better predictor of posterior CC area than VIQ_{est} and that VIQ_{est} was a better predictor of FA in the genu should be interpreted cautiously.

Conclusions

The present study found some evidence for a relationship between IQ and CC size, with smaller posterior regions of the CC being associated with higher PIQ_{est}. This finding is consistent with prior research of Allin et al. (2007) who, although it was not the focus of their study, found a similar relationship with IQ in individuals whose age was comparable to that of the current sample. Although our finding is at odds with that of Luders et al. (2007), who report that a larger posterior CC is associated with higher IQ in a sample whose mean age was about 10 years older than ours, we propose that it may reflect continued development of the CC. We also found a relationship between estimated VIQ and the integrity of the genu, once again negative in direction. These findings emphasize the need to consider the regions of the CC separately, as they not only connect different brain regions but they also appear to have different relationships with IQ and age. They also highlight the importance of measuring both CC size and integrity. Finally, this study suggests that differences in CC size can have consequences for cognitive processing. As such, it raises the possibility that atypical CC morphology observed in some clinical populations, such as multiple sclerosis (Pelletier et al. 2001), schizophrenia (Shenton et al. 2001), Alzheimer's disease (Wang et al. 2005), traumatic brain injury (Mathias et al. 2004), and attention deficit hyperactivity disorder (Giedd et al. 2001) may have implications for the cognitive profile of deficits observed in these groups.

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References

- Allin M, Nosarti C, Narberhaus A, Walshe M, Fearson S, Kalpakidou A, Wyatt J, Rifkin L, Murray R (2007) Growth of the corpus callosum in adolescents born preterm. *Arch Pediatr Adolesc Med* 161:1183–1189
- Antonini A, Berlucchi G, Marzi CA, Sprague JM (1979) Importance of corpus callosum for visual receptive fields of single neurons in cat superior colliculus. *J Neurophysiol* 42:137–152
- Axelrod BN (2002) Validity of the Wechsler abbreviated scale of intelligence and other very short forms of estimating intellectual functioning. *Assessment* 9:17–23
- Banich MT (1995) Interhemispheric interaction: mechanisms of unified processing. In: Kitterle FL (ed) *Hemispheric communication: mechanisms and models*, vol. xvi, pp 271–300. Lawrence Erlbaum, Hillsdale, 374 pp (1995)
- Banich MT (1998) The missing link: the role of interhemispheric interaction in attentional processing. *Brain Cogn* 36:128–157
- Banich MT (2003) Interaction between the hemispheres and its implications for the processing capacity of the brain. In: Davidson RJ, Hugdahl K (eds) *The asymmetrical brain*. MIT Press, Cambridge, pp 261–302
- Banich MT, Belger A (1990) Interhemispheric interaction: how do the hemispheres divide and conquer a task? *Cortex* 26:77–94
- Banich MT, Brown WS (2000) A life-span perspective on interaction between the cerebral hemispheres. *Dev Neuropsychol* 18:1–10
- Barnea-Goraly N, Menon V, Eckert M, Tamm L, Bammer R, Karchemskiy A, Dant CC, Reiss AL (2005) White matter development during childhood and adolescence: a cross-sectional diffusion tensor imaging study. *Cereb Cortex* 15:1848–1854
- Belger A, Banich MT (1992) Interhemispheric interaction affected by computational complexity. *Neuropsychologia* 30:923–929
- Belger A, Banich MT (1998) Costs and benefits of integrating information between the cerebral hemispheres: a computational perspective. *Neuropsychology* 12:380–398
- Berlucchi G (1965) Callosal activity in unrestrained, unanesthetized cats. *Arch Ital Biol* 103:623–634
- Berlucchi G (1966) Electroencephalographic studies in “split brain” cats. *Electroencephalogr Clin Neurophysiol* 20:348–356
- Berlucchi G (1972) Anatomical and physiological aspects of visual functions of corpus callosum. *Brain Res* 37:371–392
- Berlucchi G (2006) Revisiting the 1981 Nobel Prize to Roger Sperry, David Hubel, and Torsten Wiesel on the occasion of the centennial of the Prize to Golgi and Cajal. *J Hist Neurosci* 15:369–375
- Berlucchi G, Rizzolatti G (1968) Binocularly driven neurons in visual cortex of split-chiasm cats. *Science* 159:308–310
- Berlucchi G, Sprague JM, Antonini A, Simoni A (1979) Learning and interhemispheric transfer of visual pattern discriminations following unilateral suprasylvian lesions in split-chiasm cats. *Exp Brain Res* 34:551–574
- Bishop KM, Wahlsten D (1997) Sex differences in the human corpus callosum: myth or reality? *Neurosci Biobehav Rev* 21:581–601
- Caldu X, Narberhaus A, Junque C, Gimenez M, Vendrell P, Bargallo N, Segarra D, Botet F (2006) Corpus callosum size and neuropsychologic impairment in adolescents who were born preterm. *J Child Neurol* 21:406–410
- Castro-Caldas A, Miranda PC, Carmo I, Reis A, Leote F, Ribeiro C, Ducla-Soares E (1999) Influence of learning to read and write on the morphology of the corpus callosum. *Eur J Neurol* 6:23–28
- Cohen J (1988) *Statistical power analyses for the behavioral sciences*. Academic Press, New York
- Dimond SJ (1976) Depletion of attentional capacity after total commissurotomy in man. *Brain* 99:347–356
- Giedd JN, Blumenthal J, Jeffries NO, Rajapakse JC, Vaituzis AC, Liu H, Berry YC, Tobin M, Nelson J, Castellanos FX (1999) Devel-

- opment of the human corpus callosum during childhood and adolescence: a longitudinal MRI study. *Prog Neuropsychopharmacol Biol Psychiatry* 23:571–588
- Giedd JN, Blumenthal J, Molloy E, Castellanos F (2001) Brain imaging of attention deficit/hyperactivity disorder. In: Wolf LE, Wasserstein J et al (eds) *Adult attention deficit disorder: brain mechanisms and life outcomes*, vol x, pp 33–49. New York Academy of Sciences, New York, 409 pp
- Haier RJ, Jung RE, Yeo RA, Head K, Alkire MT (2004) Structural brain variation and general intelligence. *Neuroimage* 23:425–433
- Haier RJ, Jung RE, Yeo RA, Head K, Alkire MT (2005) The neuroanatomy of general intelligence: sex matters. *Neuroimage* 25:320–327
- Hofer S, Frahm J (2006) Topography of the human corpus callosum revisited—comprehensive fiber tractography using diffusion tensor magnetic resonance imaging. *Neuroimage* 32:989–994
- Hoptman MJ, Davidson RJ (1994) How and why do the two cerebral hemispheres interact? *Psychol Bull* 116:195–219
- Hulshoff Pol HE, Schnack HG, Posthuma D, Mandl RC, Baare WF, van Oel C, van Haren NE, Collins DL, Evans AC, Amunts K, Burgel U, Zilles K, de Geus E, Boomsma DI, Kahn RS (2006) Genetic contributions to human brain morphology and intelligence. *J Neurosci* 26:10235–10242
- Hutchinson AD, Mathias JL, Banich MT (2008) Corpus callosum morphology in children and adolescents with attention deficit hyperactivity disorder: a meta-analytic review. *Neuropsychology* 22:341–349
- Hynd GW, Semrud Clikeman M, Lorys AR, Novey ES et al (1991) Corpus callosum morphology in attention deficit-hyperactivity disorder: morphometric analysis of MRI. *J Learn Disabil* 24:141–146
- Innocenti GM, Bressoud R (2003) Callosal axons and their development. In: Iacoboni M, Zaidel E (eds) *The parallel brain: the cognitive neuroscience of the corpus callosum*. MIT Press, Cambridge, pp 11–26
- Kreuter C, Kinsbourne M, Trevarthen C (1972) Are disconnected cerebral hemispheres independent channels? A preliminary study of the effect of unilateral loading on bilateral finger tapping. *Neuropsychologia* 10:453–461
- Luders E, Narr KL, Bilder RM, Thompson PM, Szeszko PR, Hamilton L, Toga AW (2007) Positive correlations between corpus callosum thickness and intelligence. *Neuroimage* 37:1457–1464
- Mathias JL, Bigler ED, Jones NR, Bowden SC, Barrett-Woodbridge M, Brown GC, Taylor DJ (2004) Neuropsychological and information processing performance and its relationship to white matter changes following moderate and severe traumatic brain injury: a preliminary study. *Appl Neuropsychol* 11:134–152
- Miyata J, Hirao K, Namiki C, Fukuyama H, Okada T, Miki Y, Hayashi T, Murai T (2007) Interfrontal commissural abnormality in schizophrenia: tractography-assisted callosal parcellation. *Schizophr Res* 97:236–241
- Narberhaus A, Segarra D, Caldu X, Gimenez M, Junque C, Pueyo R, Botet F (2007) Gestational age at preterm birth in relation to corpus callosum and general cognitive outcome in adolescents. *J Child Neurol* 22:761–765
- Nosarti C, Rushe TM, Woodruff PW, Stewart AL, Rifkin L, Murray RM (2004) Corpus callosum size and very preterm birth: relationship to neuropsychological outcome. *Brain* 127:2080–2089
- Osawa A, Maeshima S, Kubo K, Itakura T (2006) Neuropsychological deficits associated with a tumour in the posterior corpus callosum: a report of two cases. *Brain Inj* 20:673–676
- Pelletier J, Suchet L, Witjas T, Habib M, Guttman CR, Salamon G, Lyon-Caen O, Cherif AA (2001) A longitudinal study of callosal atrophy and interhemispheric dysfunction in relapsing-remitting multiple sclerosis. *Arch Neurol* 58:105–111
- Peru A, Beltramello A, Moro V, Sattibaldi L, Berlucchi G (2003) Temporary and permanent signs of interhemispheric disconnection after traumatic brain injury. *Neuropsychologia* 41:634–643
- Peterson BS, Feineigle PA, Staib LH, Gore JC (2001) Automated measurement of latent morphological features in the human corpus callosum. *Hum Brain Mapp* 12:232–245
- Peterson BS, Vohr B, Staib LH, Cannistraci CJ, Dolberg A, Schneider KC, Katz KH, Westerveld M, Sparrow S, Anderson AW, Duncan CC, Makuch RW, Gore JC, Ment LR (2000) Regional brain volume abnormalities and long-term cognitive outcome in preterm infants. *JAMA* 284:1939–1947
- Plomin R, Spinath FM (2004) Intelligence: genetics, genes, and genomics. *J Pers Soc Psychol* 86:112–129
- Psychological Corporation (1999) *Wechsler Abbreviated Scale of Intelligence (WASI) manual*. San Antonio, TX
- Rotarska-Jagiela A, Schonmeyer R, Oertel V, Haenschel C, Vogeley K, Linden DE (2008) The corpus callosum in schizophrenia—volume and connectivity changes affect specific regions. *Neuroimage* 39:1522–1532
- Schlaug G, Jancke L, Huang Y, Staiger JF, Steinmetz H (1995) Increased corpus callosum size in musicians. *Neuropsychologia* 33:1047–1055
- Schmithorst VJ, Wilke M (2002) Differences in white matter architecture between musicians and non-musicians: a diffusion tensor imaging study. *Neurosci Lett* 321:57–60
- Shenton ME, Dickey CC, Frumin M, McCarley RW (2001) A review of MRI findings in schizophrenia. *Schizophr Res* 49:1–52
- Smith SM, Jenkinson M, Woolrich MW, Beckmann CF, Behrens TE, Johansen-Berg H, Bannister PR, De Luca M, Drobnjak I, Flitney DE, Niazy RK, Saunders J, Vickers J, Zhang Y, De Stefano N, Brady JM, Matthews PM (2004) Advances in functional and structural MR image analysis and implementation as FSL. *Neuroimage* 23(suppl 1):S208–S219
- Smith SM, Zhang Y, Jenkinson M, Chen J, Matthews PM, Federico A, De Stefano N (2002) Accurate, robust, and automated longitudinal and cross-sectional brain change analysis. *Neuroimage* 17:479–489
- Spencer MD, Gibson RJ, Moorhead TW, Keston PM, Hoare P, Best JJ, Lawrie SM, Johnstone EC (2005) Qualitative assessment of brain anomalies in adolescents with mental retardation. *AJNR Am J Neuroradiol* 26:2691–2697
- Spencer MD, Moorhead TW, Lymer GK, Job DE, Muir WJ, Hoare P, Owens DG, Lawrie SM, Johnstone EC (2006) Structural correlates of intellectual impairment and autistic features in adolescents. *Neuroimage* 33:1136–1144
- Sperry RW, Gazzaniga MS, Bogen JE (1969) Interhemispheric relationships: the neocortical commissures; syndromes of hemispheric disconnection. In: Vinken PJ, Bruyn GW (eds) *Handbook of clinical neurology*. North Holland, Amsterdam, pp 273–290
- Strauss E, Wada J, Hunter M (1994) Callosal morphology and performance on intelligence tests. *J Clin Exp Neuropsychol* 16:79–83
- Sullivan EV, Rosenbloom MJ, Desmond JE, Pfefferbaum A (2001) Sex differences in corpus callosum size: relationship to age and intracranial size. *Neurobiol Aging* 22:603–611
- Tassinari G, Morelli M, Berlucchi G (1983) Interhemispheric transmission of information in manual and verbal reaction-time tasks. *Hum Neurobiol* 2:77–85
- Thompson PM, Giedd JN, Woods RP, MacDonald D, Evans AC, Toga AW (2000) Growth patterns in the developing brain detected by using continuum mechanical tensor maps. *Nature* 404:190–193
- Tramo MJ, Loftus WC, Stukel TA, Green RL, Weaver JB, Gazzaniga MS (1998) Brain size, head size, and intelligence quotient in monozygotic twins. *Neurology* 50:1246–1252
- Valera EM, Faraone SV, Murray KE, Seidman LJ (2006) Meta-analysis of structural imaging findings in attention-deficit/hyperactivity disorder. *Biol Psychiatry* 61:1361–1369

- Wang PJ, Saykin AJ, Flashman LA, Wishart HA, Rabin LA, Santulli RB, McHugh TL, Macdonald JW, Mamourian AC (2005) Regionally specific atrophy of the corpus callosum in AD, MCI and cognitive complaints. *Neurobiol Aging* 27(11):1613–1617
- Wechsler D (1999) Wechsler abbreviated scale of intelligence. The Psychological Corporation, San Antonio
- Weissman DH, Banich MT (1999) Global–local interference modulated by communication between the hemispheres. *J Exp Psychol Gen* 128:283–308
- Weissman DH, Banich MT (2000) The cerebral hemispheres cooperate to perform complex but not simple tasks. *Neuropsychology* 14:41–59
- Yakolev PI, Lecours P (1967) The myelogenetic cycles of regional maturation of the brain. In: Monkowski A (ed) *Regional development of the brain in early life*. Blackwell, Oxford
- Yamauchi H, Fukuyama H, Ogawa M, Ouchi Y, Kimura J (1994) Callosal atrophy in patients with lacunar infarction and extensive leukoariosis. An indicator of cognitive impairment. *Stroke* 25:1788–1793
- Zanetti MV, Soloff PH, Nicoletti MA, Hatch JP, Brambilla P, Keshavan MS, Soares JC (2007) MRI study of corpus callosum in patients with borderline personality disorder: a pilot study. *Prog Neuropsychopharmacol Biol Psychiatry* 31:1519–1525