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Sex Differences in Associations between Spatial Ability and Corpus Callosum Morphology

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Abstract

Rotating mental representations of objects is accompanied by widespread bilateral brain activations. Thus, interhemispheric communication channels may play a relevant part when engaging in mental rotation tasks. Indeed, links between mental rotation and dimensions of the corpus callosum – the brain's main commissure system – have been reported. However, existing findings are sparse and inconsistent across studies. Here we set out to further characterize the nature of any such links, including their exact location across the corpus callosum. For this purpose, we applied an advanced image analysis approach assessing callosal thickness at 100 equidistant points in a sample of 38 healthy adults (19 men, 19 women), aged between 22 and 45 years. We detected a sex interaction, with significant structure-performance relationships in women, but not in men. Specifically, better mental rotation performance was linked to a thicker female corpus callosum within regions of the callosal splenium, posterior midbody, and anterior third. These findings may suggest sex differences in problem solving strategies where in women, more than in men, stronger interhemispheric connectivity – especially between occipito-parietal, frontal, and prefrontal regions – is associated with improved task performance.

Graphical Abstract

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Conflicts of Interest

There are no actual or potential conflicts of interest.

Role of Authors

All authors had full access to the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. Conceptualization, MH and EL; Methodology, FK, DS, MH, and EL; Investigation, DS; Formal Analysis, FK and EL; Writing - Original Draft, FK, DS, MH, and EL; Writing - Review & Editing, FK, DS, MH, and EL; Visualization, FK and EL; Funding Acquisition, MH and EL.

We assessed whether there is a significant link between mental rotation performance and local callosal thickness, and whether this link is modulated by sex. Better mental rotation performance was associated with a thicker corpus callosum in female but not in male brains.

Keywords

Corpus callosum; Gender; Mental rotation; MRI; Sex

Introduction

Numerous studies have described sex differences in cognitive performance, substantiating male or female advantages in a variety of tasks (Halpern 1992). One of the most pronounced findings is an average male advantage in mentally rotating objects (Linn and Petersen 1985; Masters and Sanders 1993; Voyer et al. 1995). Mental rotation has been shown to activate a network of brain regions (for review and meta-analysis see Zacks 2008) and, notably, these activations seem to differ by sex (Butler et al. 2006; Clements-Stephens et al. 2009; Hugdahl et al. 2006; Jordan et al. 2002; Schoning et al. 2007; Thomsen et al. 2000; Weiss et al. 2003). More specifically, males have been reported to show stronger activations in parietal regions than females, whereas females have been reported to show stronger activations in frontal and inferior temporal regions than males. These sex differences have been interpreted to reflect sex differences in processing strategies, with a more “automatic” bottom-up approach in males and a more “serial” or “analytic” top-down approach in females (Butler et al. 2006; Clements-Stephens et al. 2009; Hugdahl et al. 2006; Jordan et al. 2002; Thomsen et al. 2000).

The widespread and mostly bilateral distribution of activation, as observed in both sexes, suggests a significant role of interhemispheric communication in mentally rotating objects. However, given the aforementioned sex differences in activation patterns across the cortex, somewhat different interhemispheric channels in men and women might be involved. The corpus callosum is the largest interhemispheric commissure in the human brain, connecting the hemispheres via topologically organized fiber tracts (e.g., fibers crossing anterior callosal sections connect frontal brain regions). Thus, while links between mental rotation performance and callosal size might manifest in both sexes, effect size and/or exact location across the corpus callosum might differ between the sexes. While a few studies that link mental rotation skills to callosal morphology exist (Hines et al. 1992; Martin-Loeches et al.

2013; Newman 2016), their outcomes are rather inconsistent and further research is required. Thus, to further advance this field, we applied an advanced image analysis approach assessing correlations between mental rotation performance and callosal dimensions, specifically callosal thickness, with a high regional specificity (Luders et al. 2018). We hypothesized that better performance on mental rotation tasks is associated with greater callosal thickness overall, but that there are sex differences in the location of this association given the aforementioned differences in activation patterns between males and females.

Materials and Methods

Study Sample

The subjects included in the current report ($n=38$) constitute a subsample from a larger cohort of healthy control subjects ($n=53$) recruited for a study aimed at examining brain and behavior in individuals with disorders of sex development. The current sample of 19 men and 19 women ranged between 22.37 and 45.33 years of age ($\text{mean} \pm \text{SD}$: 31.89 ± 7.02 years) and was derived as follows: First the original sample of 53 subjects was reduced by two due to excluding one subject with image artifacts and one subject who presented with widespread white matter T1-hypointensities indicative of a pathological process. The remaining sample of 51 subjects included 19 male and 32 female subjects. Given our specific hypothesis on sex differences, we aimed for a balanced design (i.e., an equal number of men and women) and thus matched the 19 males based on age with 19 females, resulting in 38 subjects.

Information on handedness was obtained using the Edinburgh Handedness Inventory, a self-report questionnaire that asks respondents to indicate which hand they prefer to use when carrying out a number of everyday activities, such as writing, throwing, and cutting with scissors (Oldfield 1971). All participants were predominantly right-handed with the exception of two men, both of whom were predominantly left-handed; and four women, one of whom was predominantly left-handed and three of whom showed no hand preference.

In regards to educational attainment, 15.8% of the participants ($n = 6$) had earned one or more GCSEs (General Certificate of Secondary Education, representing successful completion of five years of secondary education) or the equivalent; 26.4% of the participants ($n = 10$) had earned one or more A levels (representing successful completion of seven years of secondary education) or completed vocational training; 50.0% of the participants ($n = 19$) had earned an undergraduate degree; and 7.9% ($n = 3$) a postgraduate degree. NHS Health Research Authority approval (Research Ethics Committee reference 15/EM/0532) was obtained from the East Midlands - Leicester Central Research Ethics Committee, Leicester, UK, and all subjects provided their informed consent.

Cognitive Measures

Mental rotation performance was assessed using the revised Vandenberg and Kuse (Vandenberg and Kuse 1978) Mental Rotation Test (Peters et al. 1995). This test provides a measure of three-dimensional (3D) mental rotations ability, and is based on the experimental stimuli of Shepard and Metzler (1971). It requires participants to mentally rotate 3D objects,

and it consists of four practice items followed by 24 test items, divided into two sets. Three minutes are allowed for each set of 12 test items, with a one-minute rest between sets. For each item, the target stimulus is presented on the left, and participants must determine which two of four stimuli to the right are rotated versions of the target (as opposed to different shapes). Each item has two correct answers and a point is given only if both correct answers are provided. The maximum possible score is 24.

We also obtained measures of vocabulary (a proxy for general intelligence) – to be later included as a co-variate in the statistical model – using the Advanced Vocabulary Test from the Educational Testing Service Kit of Factor-Referenced Cognitive Tests (Ekstrom et al. 1976). For this test, participants choose which one of five presented words has the same, or nearly the same, meaning as a target word. Participants are awarded one point for each correct answer and lose ¼ of a point for each incorrect answer. A total of 18 target words are presented, with possible scores ranging from –4.5 to 18.

Image Data Acquisition and Preprocessing

All brain data were acquired on a Siemens 3 Tesla Skyra system with a 32-channel head coil using the following parameters: TR = 2300 ms, TE = 2.98 ms, flip angle = 9°, matrix size = 256 × 240, 176 sagittal sections, voxel size = 1 × 1 × 1 mm³. The brain images were pre-processed in SPM12 (<http://www.fil.ion.ucl.ac.uk/spm>) and the CAT12 toolbox (<http://dbm.neuro.uni-jena.de/vbm.html>) by applying corrections for magnetic field inhomogeneities and spatial alignment using rigid-body transformations. In addition, the total intracranial volume (TIV) – to be later included as a co-variate in the statistical model – was estimated (in ml) for each subject by classifying images as gray matter, white matter, and cerebrospinal fluid and adding the sub-volumes of these compartments (i.e., TIV = gray matter + white matter + cerebrospinal fluid).

Callosal Thickness Estimation

Using the preprocessed images, the corpus callosum was outlined manually in each brain's midsagittal section (Luders et al. 2007a) blind to sex, age, handedness, educational attainment, and cognitive measures (the delineation process is depicted in Supplementary Figure 1). All callosal outlines underwent a strict quality control by two experienced raters (E.L. and F.K.) independently of each other, assuring that the outlines precisely reflected the size and shape of each individual midsagittal corpus callosum. The callosal traces were extracted and automatically processed in a number of successive steps, as detailed elsewhere (Luders et al. 2018; Luders et al. 2011; Luders et al. 2014). Importantly, the callosal outlines were separated into 100 nodes and re-sampled at regular intervals rendering the discrete points comprising the two boundaries spatially uniform. Then, a new midline curve was created by calculating the 2D average from the 100 equidistant nodes representing the upper and the lower callosal boundaries. Finally, the distances between the 100 nodes of the upper as well as the lower callosal boundaries to the 100 nodes of the midline curve were calculated. These point-wise callosal distances were entered into the statistical analyses as the dependent variable.

Statistical Analyses

Sex differences with respect to the cognitive measures (i.e., mental rotation performance and vocabulary), as well as on age, handedness, educational attainment, and TIV, were assessed using independent-samples *t* tests or Mann-Whitney *U* tests, as appropriate. Effect sizes were calculated and used in conjunction with *p* values to evaluate the results. All analyses were two-tailed, with α set at 0.05.

Sex differences in callosal thickness and links between callosal thickness and mental rotation performance, including interactions with sex, were assessed using a mass-univariate general linear model, while removing the variance associated with age, vocabulary, and TIV. Significant interactions with sex were followed-up by conducting statistical tests within men and women separately. For all imaging analyses, α was set at 0.05. To control for multiple comparisons, a Monte Carlo simulation with 10,000 permutations was employed, as previously described (Luders et al. 2009).

Results

Demographics, Cognitive Measures and TIV

Descriptive statistics are summarized in Table 1. There were no significant differences between men and women in age ($t_{36} = 0.619$, $p = 0.540$, $d = 0.20$), handedness ($U = 167.50$, $p = 0.703$, $z = -0.381$), or education ($t_{36} = 0.255$, $p = 0.800$, $d = 0.08$). In contrast, there were significant sex differences in mental rotation performance ($t_{36} = 2.345$, $p = 0.025$, $d = 0.76$), vocabulary ($t_{36} = 2.248$, $p = 0.031$, $d = 0.74$), and TIV ($t_{36} = 3.363$, $p = 0.002$, $d = 1.12$), with higher scores and larger volumes in men than in women.

Callosal Thickness

The corpus callosum was thicker in men than in women in several anterior subsections, such as the rostral body and anterior midbody. However, these clusters of sex differences did not survive corrections for multiple comparisons. Thus, male and female corpora callosa seem to have similar dimensions when accounting for brain size.

Links between Mental Rotation Performance and Callosal Thickness

In the combined sample of men and women, neither positive nor negative correlations between mental rotation performance and callosal thickness survived corrections for multiple comparisons. However, significant sex interactions were apparent and these interactions survived corrections for multiple comparisons ($p = 0.048$). More specifically, significant sex differences in the association between mental rotation performance and callosal thickness became evident in three callosal clusters (see Figure 1). The significant interaction was followed up by generating cluster-specific scatterplots and confidence intervals (see Figure 1) as well as by calculating significance and correlation coefficients for men and women separately (see Figure 2). As shown in the left panel of Figure 2, within males none of the effects survived corrections for multiple comparisons (there were no significant positive or negative correlations). In contrast, as shown in the right panel of Figure 2, within females three significant clusters indicating positive correlations emerged and survived corrections for multiple comparisons ($p = 0.030$), while significant negative

correlations were absent. That is, a better female mental rotation performance was linked to a thicker female corpus callosum within splenium, posterior midbody, and anterior third, particularly at the border between genu and rostral body.

Discussion

Here we applied an advanced computational technique assessing the link between mental rotation performance and callosal thickness with a high regional specificity. We observed significant correlations in women (but not in men), with better performance linked to thicker callosal regions, specifically within the splenium, posterior midbody, and anterior third. Overall, this seems to be in accordance with theories of sex differences in cognitive strategies. Specifically, our findings may support the hypothesis that women, more than men, rely on efficient interhemispheric communication to successfully rotate objects in their minds.

The role of interhemispheric communication for mental rotation

The current results are in line with interpretations from previous studies suggesting some differences in the approaches used by men and women to solve mental rotation problems (Boone and Hegarty 2017; Butler et al. 2006; Clements-Stephens et al. 2009; Hegarty 2017; Hugdahl et al. 2006; Jordan et al. 2002; Thomsen et al. 2000). It has been suggested, for example, that men rely on a ‘gestalt’ strategy for matching shapes (also termed an “automatic” or “global” approach), which particularly involves parietal regions that are directly associated with spatial processing. Women, on the other hand, are thought to employ a series of higher-order cognitive processes related to object identification, working memory, and possibly even language representation (also termed an “analytic” approach), which engages a wide network of parietal, temporal, and frontal brain regions and presumably also interhemispheric pathways. Interestingly studies geared towards directly assessing such sex differences in strategies seem to indicate that the more automated / global shape approach is associated with a better mental rotation performance than the analytic approach (Boone and Hegarty 2017; Hegarty 2017), which is in close agreement with the outcomes of the current study where men outperformed women. Moreover, the current findings support the aforementioned assumption of sex differences in specific cognitive strategies and brain functions: That is, the sex differences in associations between mental rotation performance and callosal thickness suggest that mental rotation performance relates positively to interhemispheric communication, but only in women. In other words, better interhemispheric communication – presumably reflected as thicker corpora callosa (Luders et al. 2016; Luders et al. 2007b; Luders et al. 2018) – may improve task performance by allowing for a more effective integration of higher cognitive processes in women¹. Interestingly, the link was not evident across the entire corpus callosum, but in selected areas, including the splenium, posterior midbody, and rostral body / genu. These region-specific observations may point to an involvement of several occipital / temporal, parietal and frontal regions during mental rotation, as previously reported (Butler et al. 2006;

¹The absence of significant links in male brains does not necessarily indicate that interhemispheric communication is completely irrelevant for mental rotation in men (it just does not seem to scale with performance).

Hugdahl et al. 2006; Jordan et al. 2002; Milivojevic et al. 2009; Thomsen et al. 2000; Weiss et al. 2003; Zacks 2008), possibly engaging networks pertaining to memory, language, and object identification (Butler et al. 2006; Cabeza and Nyberg 2000; Jordan et al. 2002; Milivojevic et al. 2009).

Correspondence with other findings

Studies relating performance in mental rotation tasks to callosal anatomy are sparse and have produced inconsistent outcomes (Hines et al. 1992; Martin-Loeches et al. 2013; Newman 2016).

The first study (Hines et al. 1992) was designed to investigate links between midsagittal callosal area and mental rotation performance, verbal fluency, and language lateralization in a group of 28 women. With respect to mental rotation, the authors hypothesized a significant association within the callosal genu. Two different types of analysis were used, structural equation modeling (SEM) and principal component analysis (PCA). The PCA, but not the SEM analysis, suggested a significant positive correlation in the anterior corpus callosum (comprising of isthmus, midregion, and genu). Given that the initial hypothesis anticipated effects only within the genu, and also because of the inconsistency in results over their two analyses, the authors considered their hypothesis unsupported. However, they concluded that, although they did not find consistent support for their hypothesis, “the possibility that anterior callosal regions relate positively to visuospatial ability merits further investigation” (Hines et al. 1992; p. 12). Importantly, the present observations of positive links between mental rotation performance and callosal thickness in posterior midbody and rostral body / genu in women replicate the original findings of Hines and colleagues.

The second study (Martin-Loeches et al. 2013) focused on disentangling the relationships between callosal shape (including descriptors of thickness) and a wide variety of cognitive measures (including mental rotation). Sex differences were not examined in their sample of 50 men and 52 women, and across the whole cohort, there were no significant links between mental rotation performance and any of the callosal shape measures. This finding is consistent with the lack of significant correlations in our combined sample of men and women, despite the significant relationships we observed in women.

The third study (Newman 2016) set out to specifically investigate sex differences in 22 men and 22 women, both with respect to midsagittal callosal area and the link between mental rotation performance and corpus callosum size. Significant sex differences (men > women) were observed within the callosal rostrum and anterior midbody, albeit without applying corrections for individual brain size. Moreover, positive correlations with mental rotation performance in those same regions were reported. This latter link between task performance and callosal size was observed across the entire sample, and significant sex interactions were missing. Exploratory correlation analyses, separately within males and females, were nonetheless performed and suggested a positive correlation within the anterior midbody in men but not in women. Given the lack of brain size corrections, the unconventional statistical follow-up, and the different morphometric methods (i.e., segment-specific callosal area versus point-wise callosal thickness), the aforementioned findings are not directly comparable to the outcomes of the current study. Nevertheless, it seems notable that many of

the outcomes of the third study were not replicated here² and also seem at odds with the lack of significant correlations in the whole cohort in the study by Martin-Loeches et al. (2013), as well as with the positive associations in women observed in the study by Hines et al. (1992).

Conclusion and implications for follow-up studies

Sex differences in mentally rotating objects are well-described and scientific theories allude to the possibility of underlying sex differences in the cognitive strategies used to perform mental rotation tasks. Overall, the present findings support this hypothesis. In particular, they suggest that women, more than men, rely on efficient interhemispheric communication to successfully rotate objects in their minds. Nevertheless, the present study has some limitations. Specifically, the sample size was rather low which may have prevented the detection of less pronounced effects due to limited statistical power. Moreover, the small sample size effectively precludes any potential subset analyses contrasting, for example, left-handers versus right-handers. Interestingly, a meta-analysis of 16 studies including more than 200,000 subjects revealed a small effect of handedness on mental rotation performance favoring right-handers (Somers et al. 2015). However, no interaction with sex was found in the meta-analysis, and thus there might be no modulating impact of handedness on the effects of the current study (i.e., where handedness did not differ significantly between men and women). Finally, the small number of subjects might have resulted in some rather untypical sample characteristics, such as a lower mean vocabulary scores in females than in males. Nevertheless, while verbal ability is frequently assumed to be better in women, meta-analytic findings suggest that the sex difference in vocabulary in adults is of negligible size (Hyde and Linn 1988). Importantly, no significant associations between vocabulary score and callosal thickness were detected in the current study, and the omission of vocabulary as a covariate did not alter the results when adjusting the statistical design to explore any possible impact on the consistency of the present finding³.

In addition to replicating the current findings in a larger sample, future studies may consider complementing indicators of callosal macro-structure (e.g., point-specific callosal thickness) with estimates of callosal micro-structure (e.g., region-specific fractional anisotropy). Moreover, directly inquiring about strategies employed by participants as well as assessing associations between self-reported strategy and callosal morphology and/or brain activation may allow for additional insights. Interestingly, sex differences in mental rotation performance are already evident at preschool age (Casey et al. 2008; Hahn et al. 2010; Levine et al. 1999). Thus, future studies, preferably longitudinal in nature, investigating task performance and brain attributes will help address the origin and etiology of sex differences in mental rotation performance. It is possible, for example, that sex chromosomes or gonadal hormones during early development cause sex differences in the brain that then result in different strategies and performance on mental rotation tasks. Alternatively, performance difference between males and females may be the result of task-specific engagements, which

²However, there was good correspondence with respect to the performance measures as both studies revealed higher mental rotation scores in males than in females.

³More specifically, when vocabulary was not used as a covariate in the statistical model, the sex interaction as well as the positive correlation in females were still present, surviving corrections for multiple comparisons at $p = 0.04$ and at $p = 0.03$, respectively.

in turn might be a consequence of cultural enforcement and/or biological predisposition. In other words, boys might train their mental rotation skills by engaging in activities that require the use of these skills more often than girls do. Over time, such sex-specific engagement and training might then not only lead to average sex differences in mental rotation performance, but also to average sex differences in brain structure, as well as sex differences in links between structural brain measures and mental rotations performance measures.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Significance Statement

We assessed possible links between mental rotation performance and local callosal thickness in a sample of 19 men and 19 women. Better mental rotation performance was associated with a thicker corpus callosum in female but not in male brains. This suggests that women in particular may rely on efficient interhemispheric communication to successfully rotate objects in their minds. Overall, the findings support the hypothesis of sex differences in the cognitive strategies used to solve mental rotation tasks.

Figure 1.

Significant sex interaction for the correlation between callosal thickness and mental rotation performance. The adjusted mean callosal thickness for each of the three significance clusters (green, yellow, magenta) was extracted and plotted against the mental rotation performance scores, separately for men (blue) and women (red). Also shown are the least-square regression slopes (solid lines) and the 95% upper and lower confidence intervals (dotted lines).

Figure 2.

Correlations between callosal thickness and mental rotation performance. Shown are the findings within males only (left panel) and within females only (right panel). *Top:* Significant positive correlations (significant negative correlations were absent). Only the significance profile for females was confirmed by permutation testing ($p = 0.030$). The color bar encodes the uncorrected significance values (p). *Bottom:* Effect sizes. The color bar encodes the correlations coefficients (r), with warmer colors (yellow, orange, red) indicating positive links and colder colors (cyan, light blue, dark blue) indicating negative links.

Table 1

Descriptive sample statistics

Variable	Combined Sample (N = 38)			Males (n = 19)			Females (n = 19)		
	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
Age (years)	31.89	7.02	22.37 – 45.33	32.60	6.70	22.53 – 43.84	31.18	7.44	22.37 – 45.33
Mental Rotation ¹	11.42	4.84	1 – 20	13.16	4.60	3 – 20	9.68	4.53	1 – 17
Vocabulary ²	8.47	3.73	3 – 18	9.76	4.10	3.75 – 18.00	7.18	2.87	3.00 – 11.75
TIV (ml)	1,538	102	1,328 – 1,785	1,587	89	1,455 – 1,785	1,489	91	1,328 – 1,671

SD = Standard Deviation; TIV = Total Intracranial Volume

¹ As determined using the revised Vandenberg and Kuse (Vandenberg and Kuse 1978) Mental Rotations Test (Peters et al. 1995).

² As determined using the Advanced Vocabulary Test from the Educational Testing Service Kit of Factor-Referenced Cognitive Tests (Ekstrom et al. 1976).