Bimanual Motor Coordination in Agenesis of the Corpus Callosum

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Running Title: Bimanual Coordination in Callosal Agenesis

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Abstract

The nature and extent of deficiencies in bimanual motor coordination in individuals with agenesis of the corpus callosum (ACC) was studied using the computerized Bimanual Coordination Test (cBCT). Compared to previous bimanual tasks, the cBCT is more specifically reliant on interhemispheric interactions of lateralized motor control, allows more precise measurement, and permits examination of performance over a wider range of bimanual challenges. The cBCT performance of 13 high-functioning individuals with complete ACC was compared to 21 age- and IQmatched controls. The groups did not differ in unimanual response speed. On trials involving angled paths that require bimanual coordination, the ACC group performed significantly slower and less accurately across all angles. The largest group differences in speed occurred on trials where the hands must respond symmetrically, while mirrorimage (versus parallel) responding produced the greatest deficits in accuracy. These data confirm previous findings of deficits in bimanual coordination in callosal absence, but using significantly improved measurement technology. Deficits in bimanual coordination in ACC are present across different demands for interhand interactions in the speed and direction of movement.

Key words: agenesis of the corpus callosum, bimanual coordination, interhemispheric interactions, motor function, congenital disorders.

Introduction

Precise, synchronous coordination of the activity of the two hands is important both for routine daily tasks and for many manual skills (such as playing a musical instrument). Deficiencies in daily activities involving bimanual coordination occur with damage to the corpus callosum (Seitz et al., 2004), commissurotomy (Preilowski, 1972, 1975), and congenital absence of the corpus callosum (Jeeves, Silver, & Jacobson, 1988; Jeeves, Silver, & Milne, 1988). In order to more completely understand the impact of callosal absence on the ability to coordinate the activity of the two hands, we report a study of bimanual motor coordination in individuals with complete agenesis of the corpus callosum (ACC). We tested a larger group of individuals with ACC than any previous study, and we utilized a computerized Bimanual Coordination Test (cBCT; (Brown, 1991; Marion, Kilian, Naramor, & Brown, 2003) that is specifically reliant on interhemispheric interactions of lateralized motor control, and provides more precise measurement of the capacity to coordinate bimanually synchronous activity than previous versions of this test. Our aim was to confirm previous findings of deficits in bimanual coordination in ACC, and to shed light on the differential impact of callosal absence on various forms of inter-hand coordination. Specifically, we were interested in whether callosal absence is more detrimental for bimanual coordination tasks that require symmetric versus asymmetric hand responding; mirror image versus parallel hand movements; or either the right or left hand to respond more rapidly.

Bimanual Coordination in Callosal Disorder

The importance of interhemispheric interactions via the corpus callosum in bimanual visuomotor coordination has been suggested in studies of individuals with brain damage or disease affecting the corpus callosum. For example, failure of bilateral coupling of simultaneous finger-thumb oppositions was found in a person with an ischemic infarct of the entire corpus callosum (Seitz et al., 2004). Similarly, patients with acquired callosal damage showed diminished synchronization of bimanual rhythmical circling movements (Serrien, Nirkko, & Wiesendanger, 2001). Brown et al. (Brown, 2003; Larson, Burnison, & Brown, 2002) reported difficulty on an Etch-a-Sketch bimanual coordination task (described below) among individuals with multiple sclerosis who showed evidence of callosal involvement when tested using visual event-related potentials. Size of the corpus callosum was also found to correlate with general motor ability in school aged children who had been born prematurely (Rademaker et al., 2004).

Preilowski (Preilowski, 1972, 1975) studied bimanual coordination in two patients in whom the anterior part of the CC had been surgically severed. He used an X-Y data recorder adapted so that two large hand-cranks moved the pen – one crank moved the pen horizontally and the other moved it vertically (similar to an Etch-a-Sketch). The task required participants to draw lines through various pathways that required either unimanual or bimanual crank turning. Angled pathways required simultaneous vertical and horizontal pen movements, and therefore demanded coordinated bimanual visuomotor responding. Results indicated that the partial commissurotomy patients were not able to acquire the same level of performance with respect to either speed or accuracy as either the non-commissurotomy participants with epilepsy, or control participants.

These partial commissurotomy patients had particular difficulty maintaining their direction of pen movement on trials where the hands were required to move at different speeds and visual feedback was eliminated halfway through traversing a path. Removal of visual feedback presumably increased the demand on interhemispheric sensorimotor interactions for maintaining appropriately coordinated two-hand responding. Although involving only two patients, these findings suggest that the anterior portion of the corpus callosum is necessary for normal interhemispheric regulation of bimanual motor responding.

Difficulties have been noted in split-brain patients on other tests of bimanually coordinated activities, such as rapid alternating hand movements (Zaidel & Sperry, 1977). A study of bimanual finger-tapping in 5 commissurotomy participants found that the split-brain group was able to tap one index finger at rates comparable to controls (Kreuter, Kinsbourne, & Trevarthen, 1972). However, their performance was significantly slower than controls when performing synchronized or alternating right- and left-hand tapping movements. Similarly, individuals with partial commissurotomies were found to be deficient in the ability to make simultaneous finger movements with the two hands (Eliassen, Baynes, & Gazzaniga, 1999, 2000). The deficits in bimanual coordination seemed to be associated with surgical transection of either the anterior or posterior callosum.

Deficits in bimanual interactions have also been demonstrated in individuals with ACC. De Guise et al. (de Guise et al., 1999) tested ACC and callosotomized individuals on a serial reaction time task learned in both unimanual and bimanual conditions. They found that the ACC and split-brain participants were compromised in bimanual, but not

unimanual, learning. Persons with ACC also have been reported to be slower to transfer a motor skill (aiming movements toward the midline or ipsilateral side) from one hand/hemisphere to the other hand/hemisphere (Lassonde, Sauerwein, & Lepore, 1995). Deficiencies in tasks demanding bimanual coordination were also noted in two preschool children with ACC (Field, Ashton, & White, 1978).

Jeeves and colleagues (Jeeves, Silver, & Jacobson, 1988; Silver & Jeeves, 1994) have reported the only study of bimanual coordination in individuals with ACC using the Prelowski task. They examined bimanual coordination in two adults with complete ACC, one 11 year-old child with complete ACC, and one 11 year-old in whom the center 1/3 of the corpus callosum had been surgically severed. Using only target paths that required parallel (same direction) responding with each hand, they found that participants with ACC were slower than controls, even after prolonged practice. In addition, when visual feedback was withdrawn (after considerable practice with visual monitoring), individuals with ACC had greater difficulty than controls maintaining accurate responding on paths requiring asymmetric hand speed (one hand required to turn its crank twice as fast as the other hand). Without visual feedback, individuals with ACC tended to drift toward symmetric hand response speed. They had the most difficulty when the target pathway demanded faster responding with the left than the right hand (i.e., 112.5°). In contrast, the child with the midbody of the corpus callosum surgically severed performed normally. Although the study of Jeeves et al. involved only three individuals with ACC, when compared with the results of Preilowski, the outcome again suggests that fast, coordinated bimanual performance requires an intact anterior corpus callosum. Both studies also demonstrated that removal of the possibility of visual feedback and

monitoring is particularly detrimental in the absence of callosal interhemispheric interactions.

Franz and Fahey (Franz & Fahey, 2007) have reported absence of the normal 'bimanual cost' in three individuals with ACC. In individuals with a normal corpus callosum, bimanually synchronous simple motor reaction times are slower than unimanual RTs for either hand. This is thought to be due to bi-directional, crosshemisphere elicitation of some degree of response inhibition. In the absence of the corpus callosum, this interhemispheric inhibition would not take place and there would be no bimanual cost. This simple RT task is quite different from the BCT in that it does not include the necessity of interhemispheric modulation of ongoing response speed and integration of visual and proprioceptive feedback demanded by the BCT. Nevertheless, absence of a bimanual cost in ACC does suggest the importance of the corpus callosum in the organization of bimanual motor activity.

Bimanual Coordination and Child Development

Jeeves and colleagues (Jeeves, Silver, & Milne, 1988; Silver & Jeeves, 1994) found that younger normal children (aged 6) performed the Preilowski bimanual coordination task in a manner similar to the individuals they had tested with ACC, while older children (aged 10) were very similar in their performance to normal, non-ACC adults. They concluded that the differences in performance between 6- and 10-year-old children were due to structural maturation of callosal fibers (Giedd et al., 1999; Giedd et al., 1996).

The development of bimanual coordination in children has also been studied by a number of other investigators, using both the methodology developed by Preilowski (Fagard, 1987; Fagard, Hardy-Lâeger, Kervella, & Marks, 2001; Fagard, Morioka, & Wolff, 1985; Fagard & Peze, 1992), and an adaptation that employed an Etch-a-Sketch toy (Gladstone, Best, & Davidson, 1989; Steese-Seda, Brown, & Caetano, 1995; Tupper, 1983). In general, the outcomes of these studies have been consistent with the developmental results reported by Jeeves (Jeeves, Silver, & Milne, 1988; Silver & Jeeves, 1994). Similar developmental changes in callosal function were evident in the appearance of a bimanual cost in simple reaction times in children with a normal callosum between 4-5 years and 6-7 years of age (Franz & Fahey, 2007).

The Bimanual Coordination Test (BCT; Brown, 1991) represents a standardized test protocol for the Etch-a-Sketch adaptation of the Prelowski test. It is more likely than the original Preilowski test to yield information regarding the specific need for interhemispheric interactions in motor coordination because Preilowski's task allowed participants to use arm and wrist movements (i.e. gross motor activity), while manipulation of the knobs of the BCT is accomplished only by movements of the hands and fingers. Fine motor movements of the fingers are controlled more distinctively by the contralateral hemisphere than are arm movements, which can be more readily controlled by the ipsilateral hemisphere (Brinkman & Kuypers, 1973). Thus, the BCT should be more sensitive to the impact of callosal absence or disorder on the interhemispheric interactions that are required in the coordination of bimanual activity.

Marion et al. (Marion et al., 2003) studied development of bimanual coordination in children using a computerized version of the BCT (the cBCT). The cBCT allows more

accurate measurement of both time and errors, and therefore it is likely to be particularly sensitive to subtle changes in ability to perform bimanual motor tasks. Marion et al. tested 67 typically-developing, right-handed children between 6 and 15 years of age. Results indicated that age correlated more strongly with left hand unimanual motor speed (r = -.44) than right hand (r = -.26). Age was also strongly associated with accuracy of performance on trials demanding both symmetric (r = -.46) and asymmetric (r = -.50) bimanual responding. The correlation with asymmetric bimanual responding remained significant when co-varying performance on symmetric response trials. For symmetric responding, age was more strongly related to parallel (r = -.46) than mirror (r = -.20) responding, consistent the demonstration that mirror-image movements (i.e., similar with respect to the midline of the body) are earlier to develop than parallel movements (Fagard and Pezé, 1992; Fagard, Hardy-Legar, Karvella, & Marks, 2001). These findings of improved cBCT accuracy with age in children are presumably due to the progressive development of the corpus callosum over this age range (Giedd et al., 1999; Giedd et al., 1996).

Rationale and Hypotheses

The purpose of this study was to investigate the nature of deficits in bimanual coordination in individuals with ACC using the computerized BCT. Our investigation differed from previous studies of this question (Jeeves, Silver, & Jacobson, 1988; Silver & Jeeves, 1994) in several respects: First, we were able to test a larger group of individuals with complete ACC (n = 13), all of whom were adults (18 years or older) and relatively normally functioning (FSIQ > 80). Second, while Jeeves and colleagues gave

participants multiple training trials (9 sessions in all), we tested participants in a single session with 2 attempts at each target angle. This method is more likely to be useful in clinical neuropsychological assessments. Third, we used the BCT rather than the Preilowski task in order to force exclusive use of hands and fingers (rather than arms) for responding. Finally, we used the computerized version of the BCT in order to improve on the precision of time and error measurements.

Based on previous work, we hypothesized that, relative to age- and IQ-matched controls, individuals with ACC would: (1) not differ in unimanual right hand speed; (2) be somewhat slower on left hand unimanual trials (as was true of younger children); (3) be slower and less accurate overall on bimanual trials; (4) have relatively greater difficulty than controls when the hands were required to respond in an asymmetric manner – one hand faster than the other; (5) have relatively greater difficulty on parallel hand movements – both hands turning clockwise – than mirror-image movements – one hand clockwise and one counter-clockwise; and (6) show differentially worse performance on pathways in which visual control was removed half-way through the trial.

Methods

Participants

Participants included 13 individuals with complete ACC aged 19-55 (M=30.15, SD=10.9), all with normal intellectual functioning (FSIQ 81-122; M=97.0, SD=9.3). ACC participants included 2 left-handers (both male), and 3 of the 13 were female. The control group included 21 participants of similar age (18-51 years; M=25.8, SD=9.1) and FSIQ (85-111; M=100.0, SD=6.6). In this control group, one male participant was lefthanded, and 4 participants were female.

All ACC participants provided magnetic resonance images (12 individuals) or computer tomography (1 individual) scans and radiological reports that were assessed to confirm complete absence of the corpus callosum, as well as presence or absence of the anterior commissure (visible in the scans of 12 of 13 cases). We did not attempt to assess presence or absence of other cerebral commissures since they are difficult to visualize in clinical MRIs. Potential participants were excluded if they had a history of head trauma, more than two seizures in their lifetime, major medical conditions (i.e., cancer, heart disease, diabetes), or chronic drug or alcohol use. All of the participants with ACC were free of moderate-to-severe psychiatric or other neurological conditions. However, 3 of the 13 participants with ACC were taking psychoactive medications at the time of testing (one taking Depakote; one taking Welbutrin; and one taking a combination of Amitripytyline and Paxil). In individuals with ACC, intelligence was assessed using the Wechsler Adult Intelligence Scale III (one individual was tested as a child using the Wechsler Intelligence Scale for Children). One individual with ACC originally tested (but not included in the 13 participants with ACC described above) was dropped from this study due to BCT performance consistently more than three standard deviations worse than the ACC group mean.

Participants with ACC were found through the ACC Network Directory (Schilmoeller, 1997) and the National Organization for Disorders of the Corpus Callosum, or through families who directly inquired about our research. Adult control participants were recruited from local area community colleges, as well as through

employment agencies and classified ads. Potential control participants were screened for age and level of education. Controls were excluded for a history of major medical conditions, history of chronic drug or alcohol use or current use of psychoactive medications or drugs, traumatic brain injury, learning disabilities, and seizure disorders. Estimates of intelligence (FSIQ, VIQ, and PIQ) in control participants were obtained using the Wechsler Abbreviated Scale of Intelligence.

All ACC and control participants were given a complete explanation of the testing in person and gave consent to participate in this research by signing a consent form that also covered all aspects of a larger test battery (i.e. tests of interhemispheric sensorimotor interactions, neuropsychological abilities, psychosocial functioning, and bimanual coordination). The methods and procedures of this research were approved by the Institutional Review Board at the Travis Research Institute.

The Bimanual Coordination Test

Bimanual motor coordination was tested using the computerized version of the Bimanual Coordination Test (cBCT). This task consists of a computer program that simulates the procedure of the Etch-A-Sketch version of the BCT. The cBCT consists of six bimanual target pathways (22.5°, 45°, 67.5°, 112°, 135°, 157.5°; see Figure 1), and two unimanual paths (0°, and 90°). The task requires drawing lines through specified pathways at each of the angles (one angle per trial). The target pathway and cursor appear on a computer monitor, and the cursor is moved by knobs on a response box. The right knob controls vertical movement and the left horizontal. Cursor movement draws a line as it moves to provide visual feedback of performance. Participants' field of view is open

for exploration throughout, thereby allowing both hemispheres to access all visual information.

Each participant completed a total of 24 trials. The first four trials were always unimanual – two of each at 0° and 90°, and presented in a sequence counter-balanced across participants (ABBA). The next 20 trials involved the two sets of angled pathways: the *rightward* (45°, 22.5°, 67.5°), and the *leftward* (135°, 112°, 157.5°) angles. Participants completed ten trials in one direction, followed by 10 in the other direction, with the order (rightward and leftward) counterbalanced across subjects. The rightward angles required participants to turn both knobs simultaneously in the clockwise direction (i.e., parallel hand movements), moving the cursor through a path from the bottom left to the upper right corners of the screen (Fig. 2A). The leftward angles required participants to turn the right knob in the clockwise direction and the left knob in a counter clockwise direction (i.e., mirrored hand movements), with cursor movement from bottom right to upper left corners (Fig. 2B). As seen in Figure 2, all 3 angles of a particular orientation were visible, with the path to be negotiated highlighted.

In each set of 10 trials (rightward or leftward angles), one practice trial was first allowed at the relevant middle pathway (either 45° or 135°). Following the practice trial, six test trials were administered (2 at each of the 3 angles in that direction). The first 2 trials were always the middle pathway, followed by 2 trials each at the left-hand-faster (67.5° or 112°) and right-hand-faster (22.5° or 157.5°) angles, the order also counterbalanced across participants. Following the practice and six test trials, one additional trial at each of the 3 angles of the set (rightward or leftward) was presented where visual feedback regarding cursor position and path was turned off halfway through

the trial, and the participant was required to finish drawing the line relying solely on proprioceptive cues (i.e., "without visual control", or WOVC). The order of WOVC trials (in terms of middle, right-hand-faster, and left-hand-faster angles) followed the order of the previous trials for that block that included visual feedback. Upon completion of the first set of 10 trials (rightward or leftward), the participant was presented with the other set of ten trials.

Response time was recorded from the onset of the start signal (tone) to the point at which the participant moved the cursor past the end of the pathway. If the cursor was outside of the pathway, timing ended when the cursor reached a point perpendicular to the end of the path. For scoring and data analyses, time to complete trials was capped at 150 seconds. Accuracy was measured by integration of the area-under-the-curve between the actual line drawn by the participant and the straightest possible line down the middle of the pathway between the start point and the end of the pathway. This value represented the total deviation of the cursor from the most accurate response line (see Figure 1).

Procedure

Participants were seated in front of a computer monitor with the response box placed between the participant and the monitor. To familiarize participants with the task, and to help them orient to the use of the knobs, they were first shown an Etch-A-Sketch toy. Once it was clear that participants were familiar with the operation of the knobs of the Etch-A-Sketch, they were informed that this task requires them to use similar knobs to draw lines through pathways projected onto the computer screen. They were also

informed that they would be using either one hand at a time (i.e. for the unimanual trials) or both hands in parallel (i.e. for bimanual trials).

Participants were instructed that their forearms needed to be kept on the table in order to refrain from using more than just their fingers (i.e. they were not permitted to use large, gross-motor wrist and arm movements). In negotiating angled pathways, participants were asked to respond with both hands at the same time and to refrain from using "stair-step" movements (i.e. alternating one hand and then the other). They were instructed that upon hearing a beep from the computer, they were to move the cursor as fast as they could from the start of the path to the finish without leaving the boundaries of the path.

After completing the practice trial and set of six timed trials for a particular set (leftward or rightward angles), participants completed the WOVC trials at the same three angles. Prior to these trials they were informed that halfway through the trial the cursor would disappear, requiring the pathway to be finished without seeing the line that they were drawing. The trail ended when the invisible cursor reach a level perpendicular to the end of the target pathway, at which point the screen image disappeared. Given the greater difficulty of these trials, participants were informed that the WOVC trials would not be timed.

After completion of the first set of trials (leftward or rightward), participants were given the other set of trials (i.e. angles inclined in the other direction) following the same procedures. Total cBCT testing time for each participant was approximately 20 minutes.

Data Analyses

In cases where participants were allowed two attempts at each angle (unimanual and bimanual trials with visual monitoring), a participant's time or accuracy score for the purpose of all data analyses was the average of the two trials. For WOVC trials, the accuracy score from the single attempt was used in statistical analyses.

Group differences in unimanual motor speed (time for unimanual angles -- 0° & 90° trials) were first tested using a group-by-angle General Linear Model ANOVAs of response speed. Then, bimanual speed (i.e., response time) or accuracy (i.e., area under the curve) were tested using similar group-by-angle ANOVAs (with post hoc independent samples t-tests). To better understand the affect of ACC on different forms of bimanual performance, three planned post-hoc group-by-angle ANOVAs were used: (1) simple versus more demanding bimanual responding – comparing average performance on angles that demand asymmetric interhand modulation (22.5°, 67.5°, 112.5°, & 157.5°) versus angles demanding symmetric interhand modulation (45° & 135°); (2) responding in same versus different directions with respect to the midline of the body – comparing average performance on rightward facing angles demanding parallel movements of the hands (22.5°, 45°, & 67.5°) versus leftward facing angles demanding mirror movements of the hands (112.5°, 135°, & 157.7°); and (3) asymmetric responding demanding faster right- versus left-hand responding (right: 22.5° and 157.5°; left: 67.5° and 112.5°).

Results

Group Equivalence

ACC and control participants were not significantly different with respect to age (t(32) = 1.24, ns) and FSIQ (t(32) = -1.10, ns), nor did groups differ with respect to handedness $(X^2 = 0.08, \text{ ns})$.

Unimanual Time

Mean times for each group for completion of right and left hand unimanual trials are shown in Table 1. A group-by-hand repeated measures analysis of variance revealed no statistically significant differences for hand (F(1/32) = 1.23, ns), group (F(1/32) =0.00, ns), or hand-by-group (F(1/32) = 0.61, ns). In the ACC group, an analysis of righthand versus left-hand speed showed a trend (and reasonable effect size) indicating slower left-hand speed (F(1/12) = 3.13, p = 0.10; $\dot{\eta}_p^2$ [partial eta squared] = .207). The difference did not approach significance in controls (F(1/20) = 0.053, ns).

Bimanual Time

Group means for time to complete each bimanual angle are also shown in Table 1 and Figure 2. A group-by-angle analysis of variance, with the 6 angles treated as repeated measures, revealed significantly slower overall bimanual performance speed for individuals with ACC (F(1/32) = 4.16, p < 0.05; $\dot{\eta}_p^2 = .115$). There was a significant effect of angle (F(5/28) = 2.95, p < 0.014; $\dot{\eta}_p^2 = .084$), but the group-by-angle interactions did not reach significance (F(5/28) = 1.24, ns). Table 1 also gives the *t*-values for univariate group comparisons at each angle. While in all cases, individuals with ACC were slower than controls, the group differences were significant on the two tasks that required symmetric hand responding (45° and 135°), with a trend for the 67.5° task.

Response times for the various angles were further tested based on three planned comparisons to see if individuals with ACC were particularly slow to complete specific forms of BCT performance: (a) symmetric (45° and 135°) versus asymmetric (22.5°, 67.5°, 112.5°, and 157.5°) hand responding; (b) mirror (112.5°, 135°, and 157.5°) versus parallel (22.5°, 45°, and 67.5°) responding; and (c) faster right-hand (67.5°, 112.5°) versus left-hand (22.5°, 157.5°) responding. The results of these comparisons can be seen in the top part of Table 2. Responding to asymmetric angles took longer than responses to symmetric angles, but the other angle comparisons did not produce significant main effects. There were significant main effects of group in both the symmetric-asymmetric and parallel-mirror analyses, but not in the right-left hand comparison (that involved only asymmetric angles). There were no significant interactions between group and type of responding in any of these planned comparisons. As seen in Table 1 and noted above, among the group comparisons for individual angles, the only significant differences were on the symmetrical angles.

Bimanual Accuracy

Group means for the measure of accuracy (area under the curve) are shown at the bottom of Table 1 and Figure 2. A between-group analysis of variance, with the 6 angles treated as repeated measures, revealed a significant difference in overall accuracy between the ACC and control groups (F(1/32) = 5.93, p < 0.03. $\dot{\eta}_p^2 = .156$). There was again a significant effect of angle (F(5/160) = 9.55, p < 0.001; $\dot{\eta}_p^2 = .630$), but the group-

by-angle interactions was not significant (F(5/160) = 0.82, ns). Table 1 provides the tvalues for the univariate group comparisons at each angle. On all angles, individuals with ACC were less accurate than controls – the difference being significant for 135° and 157.5°, with a trend at 112.5° (all of these angles demanding mirror hand responding).

The accuracy data were also tested based on the same three planned comparisons described above (symmetric versus asymmetric; mirror versus parallel; and faster right-hand versus left-hand responding). The results of these comparisons can be seen in the bottom part of Table 2. As with response speed, responses to asymmetric angles were less accurate than symmetric, but the other angle comparisons did not produce significant differences in accuracy. There were main effects of group in all three analyses – the effect being smallest in the right-left angle comparison (that involved only asymmetric angles). There were no significant interactions between group and type of responding in any of these planned comparisons.

Accuracy of Bimanual Responding without Visual Monitoring

Because of the greater difficulty of this aspect of the cBCT, participants were told that they were not being timed on trials where visual monitoring of performance was eliminated (half-way along the path). Thus, only accuracy data were recorded and analyzed for these trials. The distribution of accuracy scores was significantly positively skewed due to occasional trials where the participant lost orientation, and began wandering on a trajectory other than that necessary to complete the path. Thus, scores were log-transformed prior to statistical analyses which eliminated the skew.

Mean log-transformed scores for both groups on each angle attempted can be found in Table 3. A between-group analysis of variance, with the 6 angles treated as separate variables, revealed no significant overall difference in accuracy between the ACC and control groups (F(1/32) = 0.25, ns), nor was the group-by-angle interaction significant (F(5/160) = 0.56, ns). There was a significant main effect of angle (F(5/160)= 9.03, p < .001, $\dot{\eta}_p^2 = .220$). Across both groups, asymmetric angles produced larger errors than symmetric angles, and mirror movements were more difficult than parallel. Since there were no effects of group, further analyses were not performed on these data.

Discussion

The data from this study confirm the general hypothesis that individuals with ACC have significant difficulty in coordinating actions of the two hands. Deficient performance relative to controls was found in both speed and accuracy over all angles. Statistically, there were no significant interactions between group and the various target angles within the cBCT, although ACC participants were slower than controls on symmetric trials (45° and 135°), and less accurate on trials involving mirror movements (135° and 157.5°). However, our hypotheses regarding greater difficulty in ACC versus controls when required to use parallel (versus mirror-image) or asymmetric (versus symmetric) movements were not confirmed. Our hypothesis that individuals with ACC would be less accurate than controls on trials completed without visual control was also not confirmed.

Unimanual Speed

There were no significant differences in unimanual speed between the ACC and control groups, nor was there strong evidence for a greater degree of difference between hands in individuals with ACC. The most important implication of these unimanual findings is that they rule out any contribution of specific motor system deficiencies to the deficits in ACC seen on the subsequent bimanual tasks. Diminished performance in ACC was only apparent when faced with a demand for bimanually coordinated motor activity.

The lack of differences between the right and left hand in unimanual speed for either group is somewhat surprising (although a sight trend for slower left-hand speed was evident in individuals with ACC). That handedness was not a contributor to this unexpected result was made clear by the fact that all 3 left handed individuals were in the middle of the distributions for both right- and left-hand unimanual response speed. Furthermore, eliminating left-handers had no effect on the hand, group, or group-by-hand outcome. This absence of significant effects of hand may be due to the non-skilled and automatic nature of the unimanual task, or the fact that the participants were all adults. Previous studies have found that right-left hand differences in such simple motor tasks become smaller with age throughout childhood (Kilshaw & Annett, 1983). Marion et al. (2003) found that unimanual left-hand respond speed correlated more strongly with age in children (-.439) than did right-hand speed (-.263). Thus, a greater effect of hand might be expected in studies of unimanual speed in children with ACC, but was not a significant factor in this study of adults.

Bimanual Speed

Individuals with ACC were slower than controls on all tasks requiring bimanual hand interactions. This outcome replicates deficits found in ACC (Jeeves, Silver, & Jacobson, 1988) or partial commissurotomy (Preilowski, 1972, 1975) using the Prelowski version of the bimanual coordination task. Our results are also consistent with deficiencies in ACC found for various general visual-motor tasks (Chiarello, 1980; Sauerwein, Nolin, & Lassonde, 1994; Saul & Biersner, 1977) or on other tasks specifically demanding bimanual interactions (Brown, 2003; Chicoine, Proteau, & Lassonde, 2000; Jeeves, Simpson, & Geffen, 1979; Quinn & Geffen, 1986; Sauerwein & Lassonde, 1983). Specific deficits in the speed of bimanually coordinated motor activity in individuals with ACC suggest that callosal absence results in slower computation and execution for activities where speed of movement of one hand must be modulated with respect to the speed of the other hand. Thus, these results support the claim that absence of the CC prevents the "fine tuning" of certain cognitive and motor process without substantially affecting the basic capacity to do the task (Chiarello, 1980; Sauerwein et al., 1994).

Of particular importance in the current study was the ability to compare relative deficits in individuals with ACC for different forms of inter-hand interaction. It was hypothesized that individuals with ACC would display larger deficits relative to the control group on angles requiring more difficult forms of interhemispheric modulation and integration of motor activity. We had hypothesized greater difficulty with callosal absence for asymmetric (versus symmetric) hand responding (Jeeves, Silver, & Jacobson, 1988; and Silver & Jeeves 1994). However, the group-by-angle interaction for this

comparison was not significant. Moreover, the trends were in the opposite direction. Differences between groups were more notable for symmetric than asymmetric hand responding (see Table 1). Inspection of the mean response times indicates that individuals with ACC tended to have similar response times for angles requiring symmetric and asymmetric hand movements. Control participants, on the other hand, were notably faster (and more accurate) for symmetric than asymmetric responding. It could be postulated that in the absence of the corpus callosum the two hemispheres operate independently using all available visual feedback. Thus, under conditions that do not limit visual feedback, it makes little difference in facilitating responding whether there is congruence of the movements required of each hand by the task (i.e., equal or unequal speed). However, persons with a normal corpus callosum benefit from the symmetry of response speed via interhemispheric interactions.

Another factor to consider is that the trials requiring symmetric responding are always presented prior to those requiring the same movement (parallel or mirror image) but asymmetric responding. Significant group differences for the symmetric responding and not asymmetric may indicate that individuals with ACC have a particular disadvantage when presented with a novel bimanual task – that is, they may benefit less readily from practice and take longer to adapt to the particular form of cBCT responding (rightward or leftward). This conclusion is consistent with observations in other domains of cognitive performance that individuals with ACC have particular difficulty on complex tasks when they are relatively novel (Brown, 2003; Paul et al., 2007).

When we compared speed of parallel movements (i.e., turning knobs in the same outer spatial direction, but in opposite directions with respect to the midline of the body)

to mirrored movements (i.e., movements in the same direction with respect the midline of the body), we did not find either an overall angle effect, or an interaction between angle and group. Developmental studies in children suggest notable mirroring of movements in the opposite hand during unimanual activity, as well as greater ease when performing mirrored movements compared to parallel movements. Decrease or disappearance of these phenomena as children mature has been presumed to be a result of callosal maturation (Fagard et al., 1987; Fagard & Peze, 1992; Fagard et al., 2001; and Quinn & Geffen, 1986 Lassonde, Sauerwein, & Lepore, 1995). Thus, we had presumed that callosal absence would increase the likelihood of movement mirroring, which might facilitate the ability to perform mirror-image movements on the cBCT and make parallel movements relatively more difficult. We did not find an interaction between group and this dimension of bimanual performance in either speed or accuracy. However, group comparison of accuracy for individual angles suggested that callosal absence resulted in significantly impaired performance on 2 of the 3 angles involving mirror-image movements, but none of the angles demanding parallel movements. Thus, in adults with ACC, accuracy of performance may be negatively affected by the demand for mirrorimage responding.

In our previous study of child development of bimanual coordination (presumably reflecting development of the corpus callosum), left-hand facilitation errors were more strongly correlated with age (-.492) than right-hand facilitation (-.344). Thus, it was surprising in the current study that statistically significant differences were not found involving right-hand versus left-hand facilitation trials. Neither the angle nor the group-by-angle effects were significant. This outcome was not altered by omitting left-handed

individuals from the analyses. Thus, it appears that the laterality of hand facilitation is not critical in the cBCT performance of adults. If hand dominance does play a role in bimanual coordination, it is equally important in accelerating and decelerating response speed, and therefore its role cannot be uniquely detected by the cBCT.

Bimanual Accuracy

Overall, the data for accuracy of bimanual performance reflected the same pattern of group and task differences found for speed (see Table 2) – across all bimanual challenges, individuals with ACC performed with less accuracy than controls. The similarity in outcome for both speed and accuracy indicates that the deficits in individuals with ACC seen in speed of bimanual performance were unlikely to be the result of differences between groups in strategic choices regarding speed versus accuracy. The ACC group was both slower and less accurate. Effect sizes were only slightly larger for accuracy than speed.

It is often the case that children with difficulty on timed tasks work to maximize speed at the expense of accuracy. Therefore, deficits in children with brain disorders are often seen most clearly in accuracy measures. Steese-Seda, et al. (Steese-Seda et al., 1995) found this pattern in a previous BCT test of children with ACC. However, older adults who have difficulty on a task are more likely to be cautious, with deficits apparent in speed but not accuracy. The adults with ACC tested in this research did not show either pattern in any remarkable way.

Bimanual Coordination without Visual Monitoring

When forced to negotiate the cBCT angles without visual monitoring, there were a few instances in both groups where individuals got disoriented in their movements, resulting in enormous error scores. Thus, we log-transformed the data to eliminate skew in the distributions. Contrary to expectations, there were no effects of group in analyses of these log-transformed error scores.

Previous research using the Preilowski bimanual task had found that performance without visual monitoring was particularly sensitive to deficits in partial commissurotomy (Preilowski, 1972, 1975) and in individuals with ACC (Jeeves, Silver, & Jacobson, 1988; Silver & Jeeves, 1994). Zaidel and Sperry (Zaidel & Sperry, 1977) noted that individuals with commissurotomies had difficulty doing unfamiliar bimanual actions without the aid of vision. The difference in our outcome from these prior studies may be the result of significant differences in the way the studies were conducted. Both Preilowski et al. and Jeeves et al. tested for group differences after establishing more habitual responding (via 16 prior training trials per angle for Preilowski, and 18 per angle for Jeeves). Since measures without visual monitoring were taken in our study after only 2 prior attempts at each angle, our test was much more difficult and novel for both groups. Consequently, the variance in the performance of both groups was large (even after log transformation), reducing the power of these tests to detect group differences. Further research is necessary to explore differences between groups in cBCT responding without visual monitoring.

Variances in log-transformed scores were not too great for a main effect of angle to emerge. As one might expect, angles for which one needed to maintain asymmetric

response speeds were more severely affected by removing visual monitoring than were angles demanding symmetric responding. This was due to the greater tendency to resort to symmetric hand movements when performing mirror-image hand activities without visual feedback, a result shown also by Jeeves and his colleagues (Jeeves, Silver, & Jacobson, 1988; Silver & Jeeves, 1994).

Callosal Absence and Compensatory Strategies in ACC

While the results of this research strongly support the existence of a deficit in bimanual coordination in individuals with ACC, it is not the case that such individuals cannot do the task at all. Although some participants with ACC complained about how difficult they found the cBCT, all were able to complete the various challenges of the test with reasonable, though deficient, speed and accuracy. This raises the issue of what compensatory strategies might be suggested by their cBCT performance. Chiarello (Chiarello, 1980) summarized the four most prevalent theories of compensatory mechanisms hypothesized to explain why individuals with ACC do not show a 'splitbrain syndrome': learned behavioral strategies (Gazzaniga, 1970), bilateral representation of function (Ferriss & Dorsen, 1975; Sperry, 1968, 1974), functional elaboration of ipsilateral pathways (Dennis, 1976; Reynolds & Jeeves, 1977), and increased use of noncallosal commissures (Ettlinger, Blakemore, Milner, & Wilson, 1972, 1974).

If one presumes that ACC causes the cortical motor systems controlling each hand to work independently, one behavioral strategy for persons with ACC would be to rely more heavily on visual monitoring than on proprioceptive feedback to integrate the

activity of each hand. Since participants readily moved their eyes, information surrounding the cursor would be available to both hemispheres.

On the basis of study of callosotomy patients, Franz (2003) has argued that spatial coupling of bimanual movements relies heavily on the corpus callosum, while temporal coupling appears to be much less dependent on the corpus callosum. When allowing visual monitoring of performance on a task such as the cBCT, it would appear that both spatial planning (involving visual feedback) and temporal coupling (motor and proprioceptive modulations of response speed) are required. Thus, according to Franz, overall slower and less accurate cBCT performance in ACC would be related to greater difficulty in the interhemispheric spatial coupling; and absence of external spatial coupling via removal of visual feedback would reveal the greatest deficits in ACC.

The results of Jeeves and his colleagues (Jeeves, Silver, & Jacobson, 1988; Silver & Jeeves, 1994) indicated that absence of visual feedback caused significant performance deficits to emerge in individuals with ACC, even after considerable prior training. We had hoped to also test the effect of eliminating visual feedback on earlier trials. However, without prior establishment of motor performance habits in our study, the absence of visual feedback markedly and inconsistently disrupted the performance of both groups such that the increased variance in accuracy most likely accounted for our inability to replicate this finding.

There is little evidence in the literature for equal bilateral representation of systems involved in fine motor skill (i.e., handedness) in ACC. Data suggest that the majority of individuals with ACC establish normal hand preference (Sacco, Moutard, & Fagard, 2006; Sauerwein et al., 1994), although the incidence of left handedness and

ambidexterity may be higher (Njiokiktjien & Ramaekers, 1991; Sauerwein et al., 1994). Left hemisphere dominance for motor control in ACC was supported by our data for unimanual trials. Relative to controls, individuals with ACC had somewhat greater right hand dominance, although the effect was not significant.

Based on the possibility of greater use of ipsilateral motor pathways in the absence of the corpus callosum, we had hypothesized that individuals with ACC would show less of a deficit on trials involving mirror-image responding. We had hypothesized this based on developmental data from normal children, where it has been shown that mirror movements are frequent in younger children and disappear in older children, presumably due to maturation of the corpus callosum and increased ability to inhibit ipsilateral motor activity. However, in these adult individuals with ACC, there was some evidence for the opposite outcome, i.e., greater inaccuracy in mirror-image versus parallel responding.

Finally, within the limitations of the resolution of the MRIs available from various clinical brain imaging centers, all participants with ACC appeared to have an anterior commissure, so this pathway could have served a compensatory role. It is also likely that the collicular or cerebellar commissures play some compensatory role, particularly since the task involved monitoring of a moving visual target (the cursor) and motor adjustments in response to this movement. Thus, it is very likely that noncallosal commissures play a role in the ability of individuals with ACC to accomplish the cBCT task. However, the specific role played by each noncallosal commissure in compensating for callosal absence during bimanual coordination tasks is, as yet, uncertain.

Conclusions

The results of this research strongly support the conclusion that deficits in bimanual coordination are a robust and consistent part of the syndrome accompanying ACC. As such, the results shed light on the importance of the corpus callosum in integrating and coordinating the motor activity of the two hands. The corpus callosum appears to serve a critical role in fine tuning bilateral motor functioning specifically when motor tasks must be done under time pressure, or when faced with tasks involving complex bimanual interactions.

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Table 1

-	ACC (n = 13)	Control $(n = 21)$		
Variable	M (SD)	M (SD)	t	р
	Speed Performance	e on Unimanual and Bimanu	al Angles	
Angle 0°	6.47 (2.25)	6.14 (1.62)	0.48	0.63
Angle 90°	5.65 (1.67)	6.00 (2.88)	-0.40	0.68
Angle 22.5°	19.06 (12.24)	14.12 (6.86)	1.51	0.14
Angle 45°	17.88 (11.25)	10.87 (3.48)	2.67	0.01**
Angle 67.5°	18.74 (7.25)	14.54 (6.03)	1.82	0.07
Angle 112.5°	19.11 (8.46)	15.51 (7.01)	1.34	0.18
Angle 135°	16.19 (6.90)	11.67 (4.85)	2.23	0.03*
Angle 157.5°	16.94 (6.80)	15.32 (6.35)	0.70	0.48
	Accuracy Pe	rformance on Bimanual Ang	les	
Angle 22.5°	778.4 (319.6)	720.9 (414.1)	0.42	0.67
Angle 45°	652.4 (651.3)	446.7 (190.4)	1.36	0.18
Angle 67.5°	872.6 (604.6)	681.0 (312.4)	1.21	0.23
Angle 112.5°	866.8 (431.9)	662.3 (247.3)	1.76	0.08
Angle 135°	697.3 (440.5)	373.8 (127.9)	3.18	0.03*
Angle 157.5°	1002.0 (422.8)	688.5 (293.5)	2.55	0.01**

Mean Speed (in seconds) and Error (area under the curve) of cBCT Performance for Experimental vs. Control Group Performance Measures

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

Table 2

	Angle	Group	Group x Angle
ANOVAs	F(p)	F(p)	F(p)
	Speed		
Symmetric vs. Asymmetric	13.06(0.00)**	5.23(0.02)*	2.42(0.12)
Parallel vs. Mirrored	0.00(0.93)	4.16(0.05)*	1.42(0.24)
Right vs. Left-Hand Facilitation	0.71(0.40)	2.39(0.13)	0.18(0.67)
	Accuracy		
Symmetric vs. Asymmetric	18.72(0.00)**	6.48(0.01)**	0.42(0.51)
Parallel vs. Mirrored	0.27(0.60)	5.93(0.02)*	2.14(0.15)
Right vs. Left-Hand Facilitation	0.27(0.60)	3.82(0.05)*	0.01(0.90)

BCT: Planned Post-Hoc Comparisons

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

Table 3

-	ACC (n = 13)	Control $(n = 21)$		
Variable	M (SD)	M (SD)	t	р
Angle 22.5°	2.99 (0.34)	3.04 (0.30)	-0.36	0.72
Angle 45°	2.76 (0.45)	2.76 (0.33)	-0.01	0.99
Angle 67.5°	2.99 (0.49)	3.04 (0.23)	-0.40	0.69
Angle 112.5°	3.12 (.28)	3.04 (0.32)	0.69	0.50
Angle 135°	2.92 (0.36)	2.84 (0.24)	0.72	0.48
Angle 157.5°	3.27 (0.29)	3.13 (0.31)	1.37	0.18

Mean log-transformed error scores for cBCT Performance of Experimental vs. Control Groups Performance Measures without Visual Monitoring

Figure Legends

Figure 1

<u>Schematic representation of the Bimanual Coordination Test</u>. The "response box" is a plane box with 2 knobs that is approximately the same size as an Etch-a-Sketch toy. The left knob controls horizontal cursor movement, and the right knob controls vertical. The box is plugged into the computer and controls the cursor like a mouse. Also represented are the 6 target pathways for the bimanual tasks (which appear on the computer screen). These can be grouped for analyses of performance in several ways: first by hand speed interactions: symmetrical response speed, asymmetric right-hand facilitation (right hand must respond faster than the left), and asymmetric left-hand (left hand responds faster); and second by whether the knobs must be turned in a parallel fashion (both clockwise) or in a mirror-image fashion (left counterclockwise and the right clockwise). Within each target path there is one example of a cursor path from a participant response.

Figure 2

Screen appearance for bimanual trials: (A) leftward angles and (B) rightward angles. In A the 135° angle is highlighted as the target angle for this trial; and in B, the 22.5° angle is highlighted for response.

Figure 3

<u>Means and standard deviations</u> for time (top) and accuracy (bottom) for each bimanual angle and each group.



Mirror-image movements Parallel movements





Figure 3



