

Does Handedness Affect Interhemispheric Interactions? A Lifespan Approach

By

Riti Trivedi

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Advisor: Dr. Rachael Seidler

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Abstract

The corpus callosum is a commissural tract connecting the cerebral hemispheres and influences interhemispheric interactions. Furthermore, handedness and age are thought to affect interhemispheric interactions. The corpus callosum is predicted to deteriorate as one gets older and is thought to be larger for less strongly handed people. The present study examined how degree of handedness and aging affect interhemispheric transfer time (IHTT). Handedness was assessed using questionnaires and manual dexterity tasks, while IHTT was calculated based on reaction times from the Poffenberger Paradigm and a letter matching task. The study attempts to discover if handedness and IHTT predict performance on the letter matching task in older adults (Cherbuin & Brinkman, 2006a, 2006b). We found no significant correlation between degree of handedness and IHTT for both age groups, but less strongly handed people show faster IHTT. Information from this study could be valuable for understanding how individual differences affect neurophysiology across the lifespan.

Keywords: handedness, interhemispheric interactions, age

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Although research has often focused on the neurophysiology of right-hand dominant individuals, out of every 10 to 20 people in Western populations, one is left-handed (Galobardes, Bernstein, and Morabia, 1999). Left-handed individuals have slightly different brain organization than those who are right-handed. For example, diffusion tensor imaging data reveal that left-handers have higher fractional anisotropy and lower mean diffusivity in the callosum; this may indicate more connectivity between the hemispheres in comparison to right-handers (Westerhausen et al., 2004). Also, evidence from post-mortem studies revealed that left-handed people and mixed-handers have larger corpus callosa, specifically in the midsagittal area (Witelson, 1985) that connects the sensorimotor cortices.

Previous research has found that the time it takes for information to travel between the two brain hemispheres varies with handedness. In particular, interhemispheric transfer time (IHTT), the time it takes for information to travel between the brain's right and left hemispheres, varies between handedness groups (Cherbuin & Brinkman, 2006). IHTT is thought to be closely related to the corpus callosum, the bundle of white matter that connects the right and left hemispheres of the brain and allows them to communicate with each other (Cherbuin & Brinkman, 2006). One can recruit resources from the hemispheres more efficiently with faster IHTT, which represents the functionality of the corpus callosum (Cherbuin & Brinkman, 2006). Increased callosal fiber density likely leads to faster IHTT (Cherbuin & Brinkman, 2006). Using the Poffenberger Paradigm (PP) to measure IHTT and questionnaires to quantify handedness, research has shown that left-handers and right-handers may have different interhemispheric interactions (Cherbuin & Brinkman, 2006a, 2006b). To support the theory that IHTT in the PP is

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mediated by the corpus callosum, it has been found that split-brain patients can perform the PP but at a significantly slower rate than healthy controls (Zaidel & Iacoboni, 2003). These patients do not show activity in parietal brain regions, while healthy controls do, indicating that the patients probably use subcortical regions for hemispheric information transfer (Marzi et al., 1999). Based on an earlier study of young adults by our lab, degree of handedness significantly correlates with IHTT; that is, more strongly handed subjects have slower IHTTs (Bernard & Seidler, 2008). Furthermore, left-handers typically have more efficient interhemispheric interactions than right-handers based on measurements from the letter matching task (Cherbuin & Brinkman, 2006a, 2006b). Additionally, using the PP, studies have shown that left-handers have faster IHTT than right-handers (Marzi et al., 1991).

In addition to handedness, it appears that age also affects interhemispheric interactions. Jeeves and Moes (1996) studied the differences in interhemispheric transfer time between young and elderly subjects using a computer task in which subjects had to press a button with their right or left index finger in response to stimuli presented in either the right or left visual field (Jeeves & Moes, 1996). In this task, the PP, interhemispheric transfer time was found as the difference in reaction times between responses to stimuli contralateral to the responding hand and responses to stimuli ipsilateral to the responding hand (Poffenberger, 1912). As compared to younger adults, they found that older adults had an overall larger crossed-uncrossed difference (CUD), an index for interhemispheric transfer time based on differences in reaction time to stimuli appearing in the visual field contralateral and ipsilateral to the responding hand (Jeeves & Moes, 1996). In order to make generalizations regarding the neurological basis for interhemispheric interactions for the population, it is important to understand the differences in brain organization using various population samples.

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Interhemispheric transfer can also be measured with another task involving letter matching, such as that used in Reuter-Lorenz, Stanczak, and Miller (1999). Reuter-Lorenz and her colleagues set up a task with three letters centered around a fixation cross on a computer screen. This task was a variation of that used in Cherbuin and Brinkman (2006a, 2006b) and based on the original letter matching program from Banich and Belger (1990). The participant had to establish if the target letter in the lower row matched either of the letters in the upper row. Letters that matched in the same visual field were called within-hemisphere matches, while letters matching in opposing visual fields were called across-hemisphere matches. To determine interhemispheric transfer time, they subtracted response time for within-hemisphere matches from across-hemisphere matches. Older adults were found to have a greater difference between these two times than younger adults, although the bilateral hemispheric engagement helped older adults to have better accuracy on the task relative to young adults (Reuter-Lorenz, Stanczak, & Miller, 1999).

Multiple studies have explored the relationship between IHTT and corpus callosum morphology. For instance, researchers found the white matter fractional anisotropy (FA), which measures water diffusion in white matter, in normal healthy adults ranging 40 years in age using magnetic resonance diffusion tensor imaging (DTI); they compared these values to the subjects' CUD calculated from the PP (Sullivan & Pfefferbaum, 2006). The white matter examined included the corpus callosum. Higher FA translates to a higher density of axon fibers and myelination in white matter. They found that a greater CUD was associated with lower FA indicating that more efficient IHTT correlates with greater FA. They also discovered that a greater CUD correlated with higher diffusivity in the genu, the anterior region of the corpus callosum. From these findings, they deduced that the reduction in corpus callosum

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microstructural integrity controls interhemispheric processing efficiency (Sullivan & Pfefferbaum, 2006). To gain a better understanding of brain reorganization with age, transcranial magnetic stimulation studies have found that with increasing age there is less interhemispheric inhibition (IHI) and possibly some degree of disinhibition (Talelli et al., 2008). This was evidenced by a greater degree of ipsilateral M1 activity, indicating less IHI in older adults as compared to young adults (Bernard, Trivedi, & Seidler, 2009).

Previously researchers have studied the relationships between IHTT and handedness; however, not much research has examined how the influence of degree of handedness—how strongly inclined an individual is to use a specific hand—changes with age. In the present study, we compiled degree of handedness measurements for each subject and compared the results with interhemispheric interaction data on two computer tasks, the PP and a modified letter matching task (Compton, Costello, & Diepold, 2004; Cherbuin & Brinkman, 2006; Banich & Belger, 1990); we then examined these correlations. Our goal is to replicate the finding that less strongly handed individuals have faster interhemispheric interactions and to determine whether this relationship holds with older adults. We also want to discover if IHTT predicts performance on the letter matching task in older adults as it does in young adults.

We hypothesize that less strongly handed individuals would have faster interhemispheric interactions (Bernard, Taylor, & Seidler, under revision). Furthermore, we predicted that older adults would have slower interhemispheric interactions due to deterioration of the corpus callosum across the lifespan (Sullivan & Pfefferbaum, 2006). Subjects' performance on the letter matching task is expected to correlate with their IHTT calculated from the PP. We tested

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these hypotheses by having young adults (19-30), as well as older adults (65-79) complete handedness assessments, the PP and a letter matching task.

Methods

Experiment 1

Participants

15 young adults (20-39, 23 ± 3 , 6 male, 6 LH) and 17 older adults (66-79, 73 ± 4.5 , 8 male, 4 LH) were recruited from the University of Michigan and greater Ann Arbor community. All participants signed an IRB approved consent form before beginning the experiment. The young adults were primarily students from the University of Michigan campus who responded to flyers or postings. The older adults were recruited using the Claude D. Pepper Center Older Adult Database and the UM-Engage website. Older adults were excluded for history of stroke, neurological damage, or arthritis affecting hand/fingers. All subjects were paid for their participation.

Procedure

A Dell Optiplex 755 computer with E-Prime software (Psychology Software Tools) was used for stimulus presentation and data acquisition. In a dimly lit room, each participant sat in a computer chair and put his or her head in a chin rest at a comfortable height. The chin rest was

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located at a fixed distance (55 cm) from the computer screen for all participants. The lights were dimmed to relieve eye-strain from staring at the computer screen. The PP and handedness assessments were performed in the same room in the laboratory supervised by one of the researchers.

Poffenberger Paradigm. The methodology was similar to that used in Jeeves and Moes (1995). This method allowed us to calculate specific visuomotor reaction times. In the experiment, each subject was given a computerized version of the PP. Stimuli were presented for 50 ms at 6.02° of visual angle laterally from a centrally located fixation cross. Subjects responded by tapping their index finger on a Serial Response Box (Psychology Software Tools) located on the midline. We then calculated the ‘crossed’ pathway, which was the response time to stimuli on the screen contralateral (opposite) to the responding hand by using stimulus reception from one hemisphere and motor execution in the other (Jeeves & Moes, 1995). The reverse was the ‘uncrossed’ pathway, referring to no signals crossing the corpus callosum and involving only one hemisphere for both stimulus perception and motor execution (Jeeves & Moes, 1995). The crossed-uncrossed difference, called CUD, was calculated providing an index of IHTT.

Subjects performed 800 trials total with 400 trials per hand. Subjects were allowed to practice briefly before beginning the task to ensure that all instructions were clear. The task was divided into 4 blocks. The order of blocks was counterbalanced by response hand across subjects. In between blocks, participants completed handedness and neuropsychological assessments (see below for more detail). The Poffenberger data were trimmed to eliminate outliers using a 3.0 standard deviation cutoff, and reaction times under 100 ms or over 1000 ms.

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The stimulus onset varied at 500, 750, or 1000 ms after fixation to prevent any anticipatory responses.

Letter matching task. Similar to Cherbuin and Brinkman, the stimuli in this task consisted of 7 capital letters and their lower case counterparts (*Aa, Bb, Ee, Ff, Gg, Hh, and Tt*) shown in 34-point Arial bold font (Cherbuin & Brinkman, 2006). Four letters were displayed in a square layout centered on a cross with the same font. The top two letters were in uppercase, while the bottom two letters were in lowercase. Each letter was displayed 2.0° of visual angle to the left or right of the central fixation cross and 2.0° above or below the central fixation cross for 200 ms. To relieve eyestrain, the letters were in white against a black background. There were three conditions: within-match, across-match, or non-match. In the within-match condition, two of the letters matched within the same visual field, whereas in the across-match conditions, letters matched on one of the diagonals (Figure 1b, c). Across-match conditions were set up in this way to reduce scanning methods that would increase the amount of horizontal matches. Only in the across-match condition does information travel across the corpus callosum. In the non-match condition, no letters matched (Figure 1a). Trials were created so that half were non-matches and half were matches. Of the matches, half were within-hemisphere matches and half were across-hemisphere matches. Subjects were given instructions on screen to use their index finger to push a button on a box located at the midline when they recognized matching letters and to refrain from button-pressing if they saw only non-matching letters. The fixation cross materialized on the screen for 700 ms and then stimuli were presented for 200 ms with a 500 ms pause after each trial. Subjects were given 800 ms to respond to the stimuli for each trial. The responding hand alternated between the left and right for each block. The task consisted of two

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sessions and each session had 12 blocks of 48 trials with 24 practice trials, totaling to 600 trials per session with 192 trials per condition.

Handedness and Neuropsychological Assessments. The handedness assessments measured degree of handedness based on self-report questionnaires and manual dexterity tasks. The Edinburgh Handedness Inventory (EHI) is a questionnaire that asks subjects which hand they prefer to use and how strongly they favor that hand for a variety of manual activities, such as throwing a ball, writing, and using a knife (Oldfield, 1971). To measure manual dexterity of each hand, we used the Purdue Pegboard task (Lafayette Instrument Company). Purdue Pegboard required the subjects to place as many tiny metal pieces into consecutive holes on a board as they could in a given amount of time. Next, participants completed the Tapping on Squares and Tapping on Circles tasks for each hand to test graphomotor skills (Steingrüber, 1971). Subjects used a pen to mark as many circles or squares as possible, respectively, within a given time limit (30 seconds). They then alternated the hand used to make the marks and repeated the task. For all of these tasks we were able to calculate laterality indices using the following equation: $(R-L)/(R+L)$, where R symbolizes the right hand and L is the left hand.

Moreover, subjects were given the Mattis Dementia Rating Scale (MDRS) (Mattis 1988), which provides a general assessment of cognitive abilities, and the Mini Mental State Exam (MMSE; Folstein, Folstein, & McHugh, 1975) to screen for dementia in the older participants.. Additionally, we administered a Health and Activity Questionnaire (assessing general health status, medications, etc.) and the CHAMPS questionnaire to measure physical activity levels (Stewart et al., 2001).

Statistical Analyses

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Correlations between handedness and interhemispheric communication were evaluated using linear regression analyses using SPSS software. Independent samples T-Tests compared CUD and across-within hemisphere reaction times for young and older adults and ANOVA tests were used to compare right and left visual field reaction times and response hand in the PP.

Results

Accuracy on the letter matching task was too low to measure reliable IHTT. As a result we were unable to measure correlations between across-within hemisphere reaction time, CUD, and handedness. Other correlations between handedness, age, and CUD were calculated and are discussed in the Results section below.

Discussion

Because of these low accuracy levels on the letter matching task, we decided to repeat the experiment with a few modifications (see Experiment 2).

Experiment 2

To improve accuracy in the letter matching task, Experiment 1 was repeated with the following changes: response time for the letter matching task was increased to 1500 ms and subjects were given feedback after incorrect trials as well a percent accuracy evaluation at the end of each block. Because subjects, specifically older adults, on average performed at chance

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level in Experiment 1, we implemented these changes to increase accuracy on the letter matching task. For this experiment we used 6 younger adults (19-28, 25 ± 4 , 4 male, 0 LH) and 5 older adults (65-79, 70 ± 6 , 3 male, 1 LH). Except for the modified timing in the letter matching task, participants performed the same tasks as in Experiment 1.

Results

Table 1 shows the means and standard deviation of scores on the handedness assessments based on self-reported hand preference. All of the handedness assessments were significantly correlated with one another when pooled with the exception of the Grip Strength and Purdue Pegboard measures (Table 2). Figure 2 shows the distribution of handedness scores for all participants separated by age using Edinburgh Handedness Inventory (EHI).

Table 3 shows mean reaction times for the left and right visual field stimulus presentations blocked by responding hand. There were no significant differences in reaction time for left ($F_{(1,22)}=0.035$, $p>.05$) or right ($F_{(1,50)}=0.236$, $p>.05$) hand responses to stimuli presented in either visual field. Furthermore, there were no differences for left and right-handers for responses presented in the left visual field ($F_{(1,36)}=0.000$, $p>.05$) or the right visual field ($F_{(1,36)}=0.046$, $p>.05$).

The mean CUD for young adult participants was 2.48 ± 4 ms and 3.12 ± 6.5 ms for older adults, which is consistent with previous findings (Marzi et al., 1991). There was not a significant difference in CUD for young and older adults ($F_{(1,38)}=0.376$, $p>.05$). IHTT as measured by the CUD was compared across handedness groups and there was no significant

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differences between left and right-handers ($F_{(1,36)}=0.046$, $p>.05$). This correlation was examined for young adults ($F_{(1,20)}=0.133$, $p>.05$) and older adults ($F_{(1,16)}=0.010$, $p>.05$). Regression analysis of the CUD and handedness scores showed that there was a non-significant linear relationship with handedness measured by Tap Squares for young adults ($r=0.163$, $p>.05$; Figure 3a) and Purdue Pegboard latencies for older adults ($r=0.123$, $p>.05$; Figure 3b).

Although no clear correlations were found between handedness and CUD, associations between DOMCUD, time for transfer of information from the non-dominant to dominant hemisphere, and NONCUD, time for information transfer from the dominant to non-dominant hemisphere, and handedness. The relationship between DOMCUD and handedness for young adults was significant and non-significant for older adults as indexed by Tap Circles (young adults: $r=0.52$, $p<.05$; older adults: $r=0.25$, $p>.05$; Figure 3a), indicating that less strongly handed young adults have faster transfer from the non-dominant to dominant hemisphere. We also found a significant positive linear relationship between NONCUD and handedness for young adults and a non-significant linear relationship for older adults as indexed by Tap Circles (young adults: $r=0.463$, $p<.05$; older adults: $r=0.388$, $p>.05$; Figure 3b), indicating that less strongly handed young adults have faster transfer from the dominant to non-dominant hemisphere. The graphs show opposite trends between young and older adults for DOMCUD and NONCUD versus Tap Circles (Figure 4a, 4b).

Additionally, across-within reaction times for the letter matching task were compared to CUD for young and older adults who had accuracy levels above 60% for both within and across match trials; a significant linear relationship was found between these values ($r=0.694$, $p<.05$; Figure 5a). This relationship was looked at for young adults ($r=0.461$, $p=.08$; Figure 5b) and

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older adults ($r=0.883$, $p<.05$; Figure 5b) separately. Handedness as indexed by Tap Circles was compared to across-within reaction times for all subjects ($r=0.043$, $p>.05$). No significant relationship was found, although there was a slight trend for less strongly handed individuals to have faster reaction times. Furthermore, the mean across-within hemisphere reaction time for older adults was 14.16 ± 42 ms and -3.83 ± 22 ms for young adults. There was a non-significant difference in across-within hemisphere reaction times between young and older adults ($F_{(1,23)}=1.940$, $p>.05$), although average reaction time was higher for older adults. Improvement in accuracy from Experiment 1 to Experiment 2 is visible in Table 4.

Discussion

Little work has been done to assess effects of degree of handedness on neuromotor behavior (Marzi, Bisiacchi, & Nicoletti, 1991, as cited in Bernard & Seidler, 2008). The current study impacts a broad population because people of all types of handedness were assessed. Examining IHTT developmentally as well as its dependence on handedness is beneficial for several reasons. First, understanding how IHTT, and thus the corpus callosum (Jeeves & Moes, 1995), changes with age can better our methods of treating individuals with neural diseases, which are most profound in old age (Gist & Hetzel, 2004). According to the Census 2000, 35 million people in the United States were over 65 years of age (Gist & Hetzel, 2004). Additionally, the proportion of older people in the labor force has steadily decreased (Gist & Hetzel, 2004). This steady decrease in the workforce may be due to motor cortical deficiencies considering that 28.6% of employed old adults had some type of physical disability, such as limitations on reaching, lifting, or carrying (Gist & Hetzel, 2004). Additionally, 10.8% of the

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older adult population had mental disabilities, such as problems with learning, remembering or concentrating (Gist & Hetzel, 2004). Considering the significantly large amount of older adults in the American population, it is important to learn effective strategies to improve rehabilitation of age-related neural disorders. IHTT has potential implications for how we go about rehabilitating older adults because of its relation to one's neurophysiology.

Contrary to what we expected, our study did not find significant correlations between interhemispheric transfer time and degree of handedness. Specifically, those young adults with faster transfer from the dominant to the non-dominant hemisphere (NONCUD) were typically less strongly handed. No other significant relationships were found, although we saw a similar trend with old adults and for both groups in relation to DOMCUD, transfer from the non-dominant to the dominant hemisphere. Our data indicated that values for NONCUD and DOMCUD are different across handedness groups and tend to be near zero for less strongly handed individuals. DOMCUD tends to be negative for right-handed young adults and positive for left-handed young adults; we see opposite correlations for NONCUD; asymmetry in IHTT was also found in Marzi et al. (1991). This study also found negative CUDs, similar to our study, possibly due to more bilateral activity. As a result, synchronized processing in both hemispheres rather than single hemispheric processing may be more efficient, causing negative CUDs (Marzi et al., 1991).

Furthermore, IHTT was examined in the form of across-within hemisphere reaction time in the letter matching task. Extending the possible trial response times in the task significantly improved accuracy levels in match conditions (Table 4). No strong correlations were seen

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between handedness and accuracy on the task, similar to findings of Cherbuin and Brinkman (2006). Accuracy was greater for young adults compared to older adults in both experiments.

Additionally, we found a strong correlation between CUD and across-within hemisphere reaction time from the letter matching task. This may indicate that both are reliable indices of IHTT. Although we did not see any significant correlations between across-within hemisphere reaction time and degree of handedness, this was likely due to the small sample size. To improve the accuracy for older adults on the letter matching task, in the future it may be beneficial to further increase the trial response time. Studies have shown that aging results in a reduction of interhemispheric inhibition, which enhances bilateral hemispheric processing (Talelli et al., 2008). This may lead to faster CUDs for older adults, overcoming the effects of callosal atrophy and explaining why we do not see a significant difference in CUDs between young and older adults. To compensate for callosal atrophy due to aging, Kramer and colleagues have found that an aerobic exercise intervention results in greater anterior callosal volume in older adults (Colcombe et al., 2006). This suggests a possible intervention route for improving interhemispheric interactions in older adults.

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Tables

Table 1.

<i>Handedness Measures</i>	<i>YA LH</i>	<i>OA LH</i>	<i>YA RH</i>	<i>OA RH</i>
Edinburgh	-0.40 ± 0.38	-0.57 + 0.39	0.68 ± 0.14	0.83 + 0.14
Tapping Circles	-0.11 + 0.072	-0.059 + 0.092	0.14 + 0.055	0.17 + 0.055
Tapping Squares	-0.083 + 0.025	-0.049 + 0.078	0.11 + 0.050	0.11 + 0.053
Purdue Pegboard	-0.043 + 0.065	0.012 + 0.036	0.038 + 0.040	0.030 + 0.041
Grip Strength	0.022 + 0.032	0.011 + 0.044	0.033 + 0.044	0.011 + 0.070

Mean scores (\pm SD) for self-report left and right handed participants on all handedness assessments.

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Table 2.

	Edinburgh	Tapping Circles	Tapping Squares	Purdue Pegboard	Grip Strength
Edinburgh	1	0.885***	.795***	0.418**	0.058
Tapping Circles		1	.866***	0.406*	0.08
Tapping Squares			1	.497*	0.096
Purdue Pegboard				1	0.064
Grip Strength					1

Handedness Correlations. Significance of correlations is indicated (* $p < .05$, ** $p < .01$,

*** $p < .001$).

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Table 3.

	<i>Left Visual Field Presentation</i>		<i>Right Visual Field Presentation</i>	
	<i>YA</i>	<i>OA</i>	<i>YA</i>	<i>OA</i>
<i>Left-Handers</i>	216.60 ± 16.78	288.31 ± 38.91	224.79 ± 15.56	284.50 ± 31.06
<i>Right-Handers</i>	211.73 ± 51.83	271.40 ± 55.86	219.19 ± 54.30	276.10 ± 51.56

Mean Crossed-Uncrossed Differences from Poffenberger Paradigm in milliseconds (\pm SD) based on visual field of stimulus presentation, hand preference, and age.

HANDEDNESS AND AGING AFFECT INTERHEMISPHERIC INTERACTIONS?

Table 4.

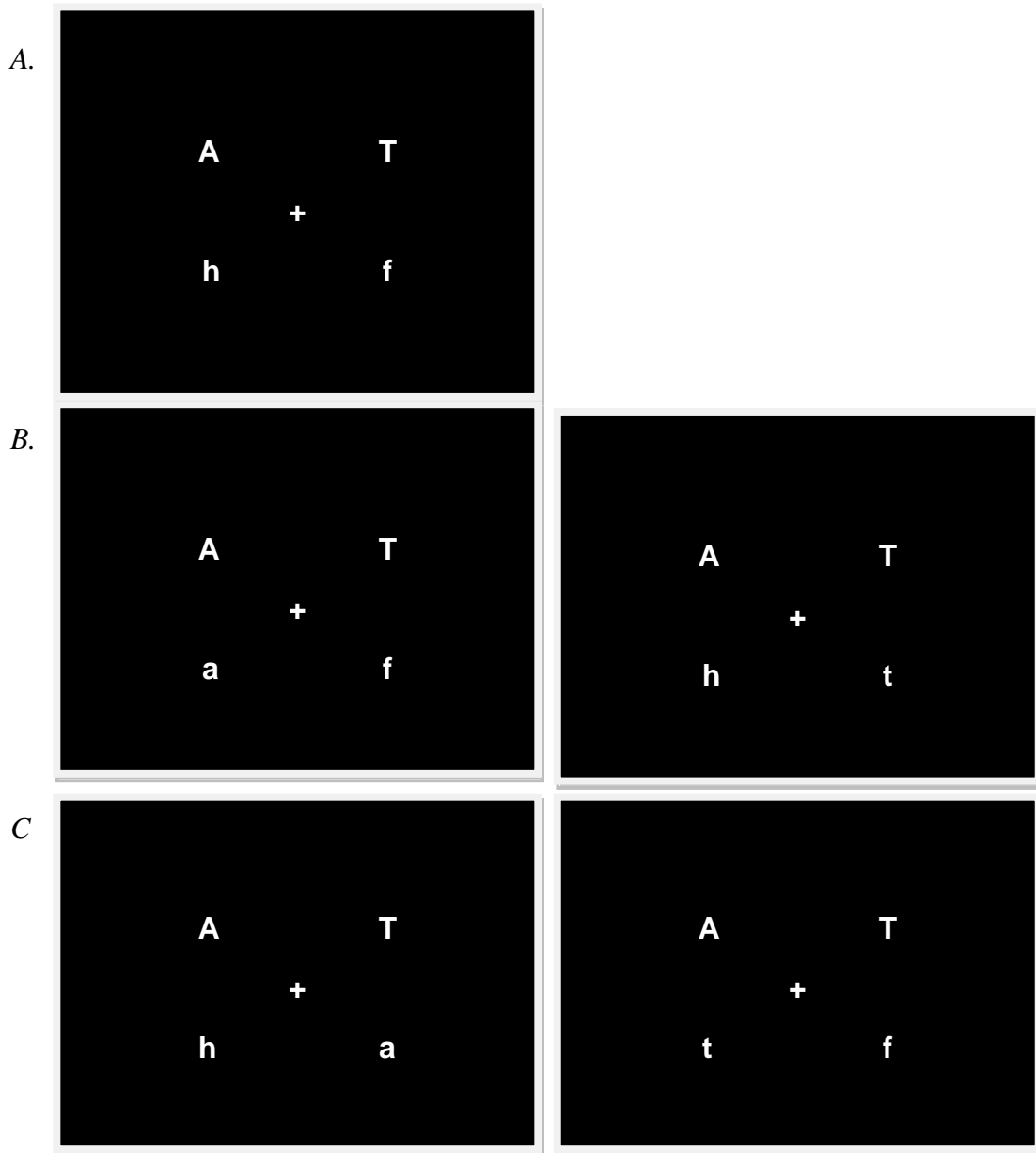
	<i>Experiment 1</i>		<i>Experiment 2</i>	
	<i>YA</i>	<i>OA</i>	<i>YA</i>	<i>OA</i>
<i>Across Accuracy</i>	0.520457	0.192146	0.90162	0.71441
<i>Within Accuracy</i>	0.603683	0.310284	0.893519	0.732639

Accuracy on letter matching task separated by experiment and age groups. A large improvement in accuracy is seen in Experiment 2 on both within and across match conditions due to alterations in acceptable trial response times.

HANDEDNESS AND AGING AFFECT INTERHEMISPHERIC INTERACTIONS?

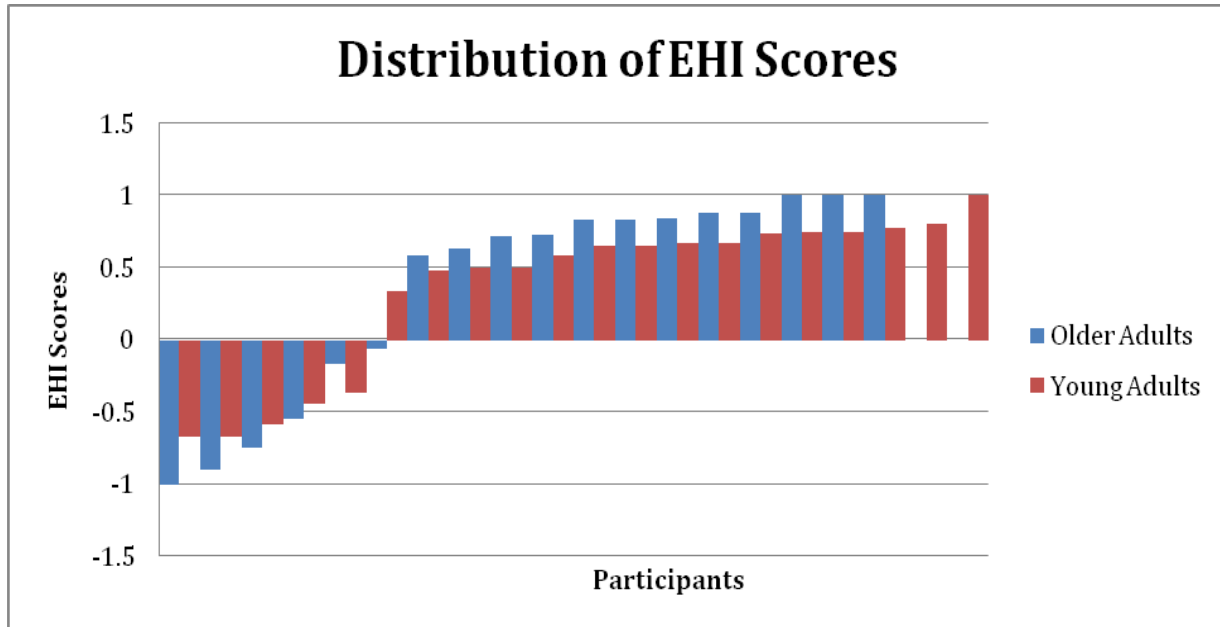
Figures

Figure 1.



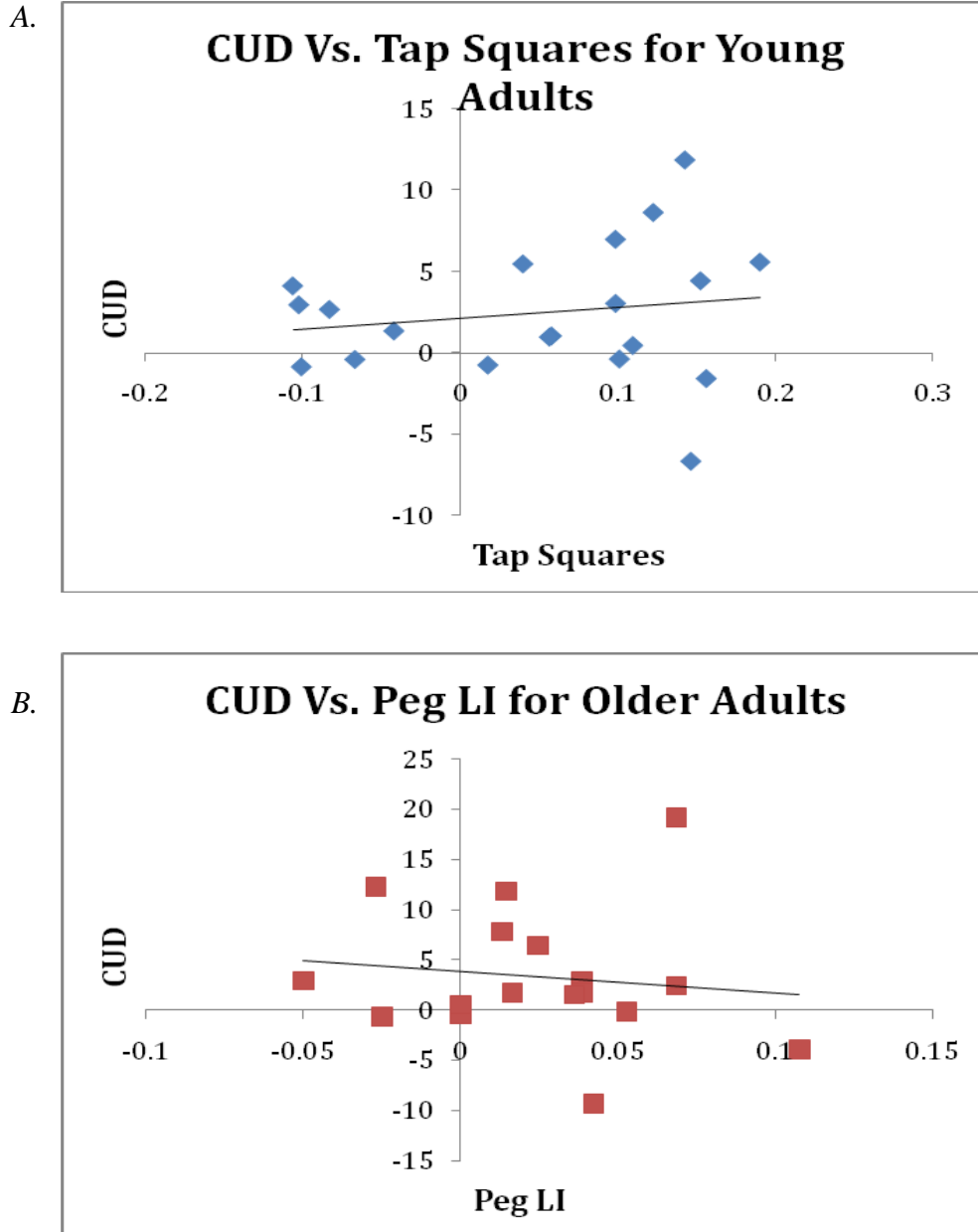
Letter match conditions. A. Non-match condition. B. Within-match conditions. C. Across-match conditions.

Figure 2.



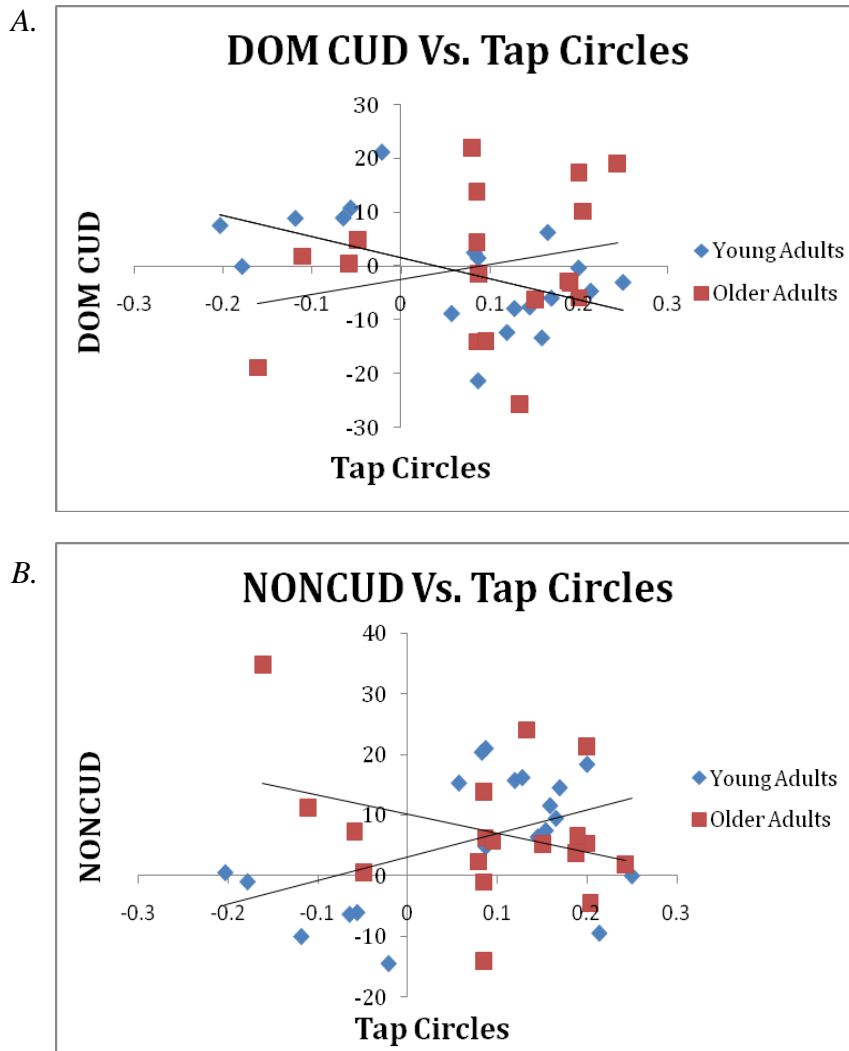
Distribution of Edinburgh Handedness Inventory scores separated by age. Older adults seem to have scores with greater deviation from zero than young adults.

Figure 3.



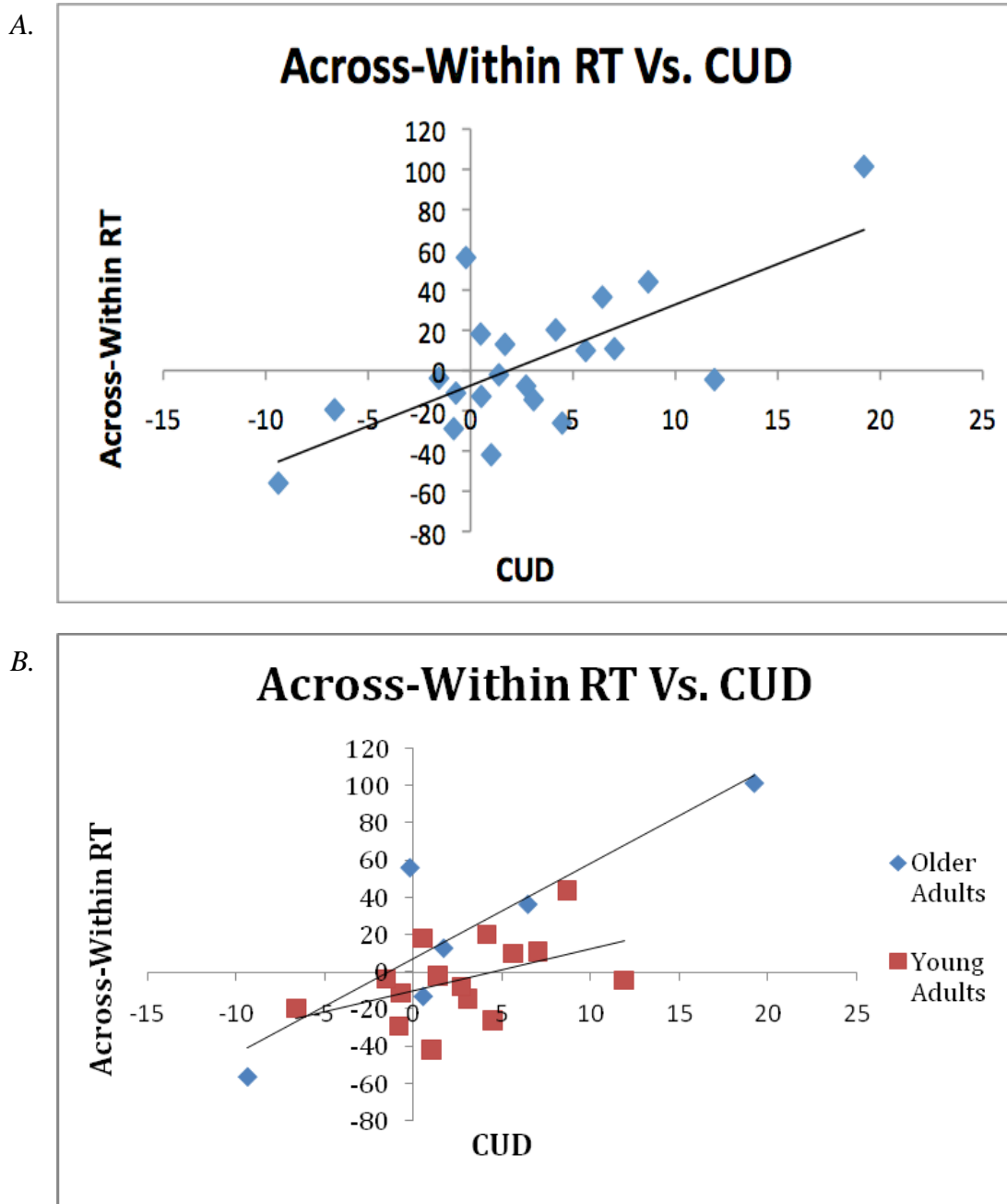
A. Crossed-Uncrossed Difference (CUD) in milliseconds versus Tap Squares for young adults. A slightly positive linear correlation is seen between this IHTT measure and handedness score. B. CUD in milliseconds versus Purdue Pegboard latencies for older adults. A small negative linear correlation is seen.

Figure 4.



A. Graph of Dominant CUD in milliseconds versus Tap Circles for young and older adults. B. Graph of Non-dominant CUD in milliseconds versus Tap Circles for young and older adults.

Figure 5.



Graph of across-within reaction times for the letter matching task versus CUD in milliseconds.

A. All subjects. B. Subjects separated by age group.