Journal of Deaf Studies and Deaf Education, 2020, 1–12

doi: 10.1093/deafed/enaa030
Empirical Manuscript

EMPIRICAL MANUSCRIPT

A Positive Relationship Between Sign Language Comprehension and Mental Rotation Abilities

Emily Kubicek[1], and Lorna C. Quandt[1,2,*,†]

[1]Educational Neuroscience Program, Gallaudet University and [2]Department of Psychology, Gallaudet University

*Correspondence should be addressed to Lorna C. Quandt, Department of Psychology, Gallaudet University, 800 Florida Ave NE, Washington, DC 20002 (e-mail: Lorna.quandt@gallaudet.edu)

Abstract

Past work investigating spatial cognition suggests better mental rotation abilities for those who are fluent in a signed language. However, no prior work has assessed whether fluency is needed to achieve this performance benefit or what it may look like on the neurobiological level. We conducted an electroencephalography experiment and assessed accuracy on a classic mental rotation task given to deaf fluent signers, hearing fluent signers, hearing non-fluent signers, and hearing non-signers. Two of the main findings of the study are as follows: (1) Sign language comprehension and mental rotation abilities are positively correlated and (2) Behavioral performance differences between signers and non-signers are not clearly reflected in brain activity typically associated with mental rotation. In addition, we propose that the robust impact sign language appears to have on mental rotation abilities strongly suggests that "sign language use" should be added to future measures of spatial experiences.

Spatial thinking is the mental process of representing, analyzing, and drawing inferences from spatial relations (Uttal et al., 2013a, 2013b). Performance on spatial tasks is positively correlated with expertise in a variety of science, technology, engineering, and mathematics (STEM) disciplines such as physical sciences, geosciences, and geography (Newcombe & Shipley, 2014). In the largest longitudinal study on spatial ability to date ($N = 400{,}000$), Wai et al. (2009) found that spatial ability performance in high school reliably predicted which students would work in a STEM field over 10 years later. The likely cause of the predictive correlation between spatial ability and STEM achievement is the fact that STEM content often requires the transformations of spatial relations (Uttal et al., 2013b). The general consensus is that spatial skill is an umbrella term that encompasses spatial visualization, spatial orientation, mental rotation, and mental transformation (Sorby, 1999).

Work in the past two decades has repeatedly shown a correlation between spatial ability and academic achievement (Buckley et al., 2018; Wai et al., 2009). Although there is contention as to how or why these correlations are present, it cannot be refuted that spatial ability is malleable (Newcombe & Shipley, 2014; Weisberg & Newcombe, 2017; for recent synthesis and discussion of contention see Buckley et al., 2018). The malleability of spatial thinking has been investigated using a variety of interventions. Classroom-accessible tools such as paper-pencil activities, interactive websites, and simple changes in content descriptions have been shown to improve student spatial cognition (including higher test scores and better understanding of concepts) yet spatial cognition is still largely ignored in the American classroom.

One of the most studied factors of spatial abilities research is mental rotation performance (Estes & Felker, 2011). Mental rotation is a cognitive process in which a mental image is imagined to be rotated around an axis in three-dimensional space (Zacks, 2008). This sub-factor of spatial ability and its relationship to academic performance is of particular interest to spatial ability researchers, as many STEM fields require adeptness of visuospatial transformations in order to learn and implement foundational concepts.

[†] Lorna C. Quandt, http://orcid.org/0000-0002-0032-1918
Received April 1, 2020; revisions received June 29, 2020; accepted August 5, 2020

Mental Rotation and Sign Language Users

Sign language is a primarily visuospatial language, being produced manually and perceived visually rather than being produced orally and perceived auditorily. Sign language users are constantly manipulating and perceiving signs created in space to communicate an infinite number of complex concepts. Like gymnasts (Ozel et al., 2002), engineers, or airline pilots (Dror et al., 1993), sign language users practice rotational transformation as a part of their daily life. When learning sign language, the learner sees a sign, flips the sign up to 180° in order to properly produce it with their own hands. For example, when watching a right-handed person sign the word “KING,” the signer moves their right hand from left shoulder to right hip. If the observer were to literally mirror the signer, their production would be incorrect. To properly learn the sign, the observer must consider the signer’s perspective, rotate the movements, and map them onto their own body. Although these practices are not identical to mental rotation, which involves transforming objects in mental imagery, it is possible that the rotations integral to American Sign Language (ASL) involve some of the same underlying processes as mental rotation.

The ability to map objects in space and switch perspectives is also critical for the communication of complex concepts in ASL. When describing a physical space in ASL, an object is first labeled with a sign (e.g., couch, chair), followed by the mapping of the object’s location, orientation, and spatial relations to other objects already established in “signing space” (Emmorey, 2001). This use of space in front of the signer functions as a type of diagram, schematically depicting spatial relationships (Emmorey, 2001). However, unlike a drawn diagram, a sign language description requires that the signer and observer create and hold a mental model of spatial relations in working memory, using mental imagery. Importantly, in addition to this working memory component, observers must also continuously perform up to a 180° rotation to understand the signer’s description of space. For people who grow up consistently using sign language, this practice with rotation, in terms of sheer time spent, far surpasses any typical activities that employ spatial cognition (i.e., playing with blocks, fixing a car), any sport played, or any course taken in an attempt to improve spatial abilities. Recent work has shown that skills in mental rotation support linguistic and non-linguistic perspective-taking skills in deaf signers (Secora & Emmorey, 2020).

In several prior studies, Deaf native signers and fluent hearing signers have performed better on tests of classic mental rotation than non-signers, while also demonstrating greater accuracy in remembering object orientation, an important element in mental imagery (Emmorey et al., 1998; Keehner & Gathercole, 2007; McKee, 1987; Talbot & Haude, 1993). However, one recent study has shown that hearing non-signers and deaf native signers demonstrate similar mental rotation abilities (Secora & Emmorey, 2019; for more on this study, see Discussion). In earlier work, people who have signed consistently since birth (i.e., native signers), regardless of hearing status, have shown an enhanced ability, compared with hearing non-signers, to mentally generate complex images and to detect mirror-image reversals (Emmorey et al., 1993). Findings such as these suggest that enhanced spatial ability is not a straightforward effect of hearing status but may also come about as a result of practice with a visuospatial language (i.e., sign language; (Parasnis et al., 1996; Pyers et al., 2010).

Although neuroimaging and psychophysiological studies have shown specific changes in the visual pathways of deaf signing subjects during visual attention tasks (see Corina & Knapp, 2006) for review), no evidence exists exploring the neurobiological basis of the known mental rotation advantages in this population.

Mental Rotation and Sign Language in the Brain

Given the characteristics of sign language that heavily rely on rotation, it is no surprise that sign language and mental rotation are associated with activation in similar areas of the brain. Mental rotation has consistently been shown to recruit the areas surrounding the intraparietal sulcus as well as motor cortices (Zacks, 2008). Parietal cortices are thought to be activated during mental rotation due to the area’s demonstrated involvement in visual image transformation. Motor cortex activation during mental rotation, however, has been shown to indicate to what degree certain cognitive strategies are being used (Zacks, 2008).

More specifically, a unique activation signature in the sensorimotor cortex is the representative of motor simulation in the human brain (Bowman et al., 2017; Debnath et al., 2019; Muthukumaraswamy et al., 2004; Oberman et al., 2007; Pineda, 2005). The mu rhythm, as measured by electroencephalography (EEG), is an alpha-range frequency (8–13 Hz) that is well suited for the exploration of motor simulation due to its involvement in sensorimotor processing (Pfurtscheller et al., 2006; Quandt & Marshall, 2014; Ulloa & Pineda, 2007).

Recent EEG research has investigated cognitive strategies used during mental rotation tasks. It is hypothesized that the greater the mu desynchronization, the greater the internal motor simulation of rotating the object (Gardony et al., 2017; Horster et al., 2013). This provides insight about what kind of strategy is being used during mental rotation. For example, as mental rotation tasks increase in difficulty (i.e., larger angular disparity), mu desynchronization lessens, suggesting a reduced use of motor simulation. Concomitant to this phenomenon, parietal alpha, and frontal theta power increase, suggesting an increased use of visuospatial processing and working memory. Thus, the simpler a task, the more motor simulation (i.e., more mu desynchronization) is used, and the more difficult a task, the more analytic strategies (i.e., less mu desynchronization) are used. Less mu desynchronization during a mental rotation task suggests that an analytic strategy is taking place (e.g., counting number of blocks within a figure, comparing the shapes visually) as opposed to mentally simulating the rotation. However, some EEG studies of mental rotation have shown the opposite effect, with less event-related desynchronization related to high ability subjects and superior performance (i.e., faster reaction time (RT); (Chen et al., 2013; Riecansky & Katina, 2010). These studies attribute lessened desynchronization during mental rotation to a type of neural efficiency, suggesting that being better at mental rotation results in a lessened cognitive load during processing, and therefore less desynchronization. Thus, the exact nature of the relationship between alpha and beta frequencies and mental rotation is still being explored.

Beyond classical language areas, the motor cortex, superior parietal cortex (motor control/proprioceptive monitoring), and sensorimotor cortices, in addition to other motor-related regions that are critical for action processing are engaged during sign language production (Corina & Knapp, 2006; Corina et al., 2007; Emmorey et al., 2016; Petitto et al., 2000). The recruitment of motor cortices during sign language production is often seen along with strong parietal area involvement, which is hypothesized to be due to the visual-motoric transformation required for sign language (Bavelier et al., 2001; Emmorey et al., 2016; 2002; 2005). These brain areas have also been shown to activate for signers when tasks do not even involve sign language. Signers show behavioral facilitation (i.e., faster RTs) when comparing printed English words that have similar sign characteristics, but not similar English characteristics (Morford et al., 2011). These behavioral impacts are also seen on the neural level, as when signers read English words, sign language translations are implicitly activated (Meade et al., 2017; Quandt & Kubicek, 2018). This pattern of results suggests that the cognitive processing related to sign language use is not only utilized during explicit sign language tasks.

Given the unique overlapping biological correlates of sign language and mental rotation, it is surprising that no neuroscientific work to date has attempted to explicate the neural underpinnings of this relationship. Contrastively, multiple studies have been done on the behavioral relationship between sign language and mental rotation with overall consistent results. However, it remains that only fluent and non-signers have been studied under these behavioral spatial cognition conditions, leaving questions unanswered in terms of a discrete or continuous relationship between mental rotation and sign language abilities. Thus, research should continue to investigate sign language under a variety of conditions to explore the possible impacts sign language has on overall cognitive processing. In an effort to further explicate the relationship between sign language and non-linguistic cognitive processes, the project presented here will examine if mental rotation ability is impacted by sign language knowledge on both the behavioral and neurobiological level.

The Current Study

There are two main considerations that have been overlooked in the existing behavioral research: the establishment of fluency-based testing (as opposed to self-report) and groups with more specificity than "signing" and "non-signing." By including a quantitative measure of fluency, future investigations can make interpretations based on sign language comprehension, as opposed to reported experience or number of courses taken, truly reporting on the impact sign language fluency has on cognition. Additionally, the inclusion of groups other than "signers" (typically self-reported fluent) and "non-signers" (typically self-reported as having no exposure to sign language), such as those with intermediary sign language comprehension, can strengthen claims related to sign language fluency and cognitive benefits.

By investigating the neurobiological correlates of mental rotation in sign language users for the first time with a wide range of comprehension skills, results will shed light on the relationship between sign language knowledge and mental rotation abilities. We aimed to answer these two questions: (1) Is sign language *fluency* needed to score well on mental rotation tasks? and (2) Does sign language *fluency* affect which strategy is used during mental rotation tasks? The second of these questions allows us to address the possibility that fluent sign language users are engaging typically recruited cortices differently than non-fluent signers and non-signers, suggesting a different cognitive strategy during these tasks. To answer these questions, we designed an EEG study in which deaf fluent signers, hearing fluent signers, hearing non-fluent signers, and hearing non-signers completed mental rotation tasks, which varied in difficulty (i.e., easy and hard conditions) to induce use of multiple cognitive strategies.

Materials and Methods

Participants

To examine the effect of sign language fluency on mental rotation, we recruited 66 adult participants ages 19–53 (mean = 31.34, no significant difference between groups' ages), 44 females, 20 males, and 2 who selected "other." Nine additional participants were recruited, but were excluded for the following reasons: two indicated they were left-handed, four were deaf individuals who scored below our "fluency" cutoff (see Behavioral Measurement section below), and three were excluded due to hardware failure or artifacts in the EEG. Participants were placed into one of the following four groups: 18 deaf fluent ASL signers, 16 hearing fluent ASL signers, 17 hearing non-fluent ASL learners, and 15 hearing non-signers. Participants were placed in the deaf fluent group if the participant identified as deaf and scored 70% or higher on the American Sign Language Comprehension Test (Hauser et al., 2015; ASL-CT; see: Behavioral Measurements). Participants were placed in the hearing fluent group if they identified as hearing and scored 70% or higher on the ASL-CT. Participants were placed in the hearing non-fluent group if they identified as hearing and scored below 70% on the ASL-CT. Participants were placed in the hearing non-signing group if they identified as hearing and indicated no exposure to any sign language (i.e., Mexican Sign Language, ASL). See Figure 2 for sex demographics, ASL-CT scores by group, and average age of starting to learn sign language.

Participants signed an informed consent form presented in written English Sign Language or ASL that had been approved by the university's institutional review board. Participants were compensated $20 an hr for their time. Educational and demographic information can be found in Tables 1 and 2. We conducted a chi-square test to see if there was any significant relationship between group membership and educational level, and no significant relationship was found, X^2 $(12, N = 66) = 9.03$, $p = .70$.

To better serve our research questions, we refer to groups and subgroups in the following ways. The deaf fluent signing group, the hearing fluent signing group, the hearing non-fluent signing group, and the hearing non-signers will be referred to as Deaf-Fluent, Hearing-Fluent, Hearing Non-Fluent, and Hearing Non-Signing groups, respectively. For some hypotheses, the participant groups were combined. The Deaf-Fluent and Hearing-Fluent groups comprise the larger Fluent group. The Hearing Non-Fluent and Hearing Non-Signing groups comprise the larger Non-Skilled group.

Behavioral Measurements

Four behavioral measures were administered before the start of the EEG experiment. The first measure the participant completed was the 24-item Vandenberg and Kuse Mental Rotation Test (VK-MRT; Peters et al., 1995). The second measure given was the ASL-CT developed by Hauser et al. (2015). The ASL-CT is a 30-item multiple-choice test that measures ASL receptive skills and is administered through an online portal. The third measure administered to the participant was a Spatial Experience Survey (SpES), which is a compilation of widely used spatial experience questionnaires (Cherney & Voyer, 2009; Newcombe, Bandura, & Taylor, 1983; Terlecki & Newcombe, 2005). The last survey given was a basic background form including questions asking about college major, interests, and occupation. Basic language information was also collected, such as primary language use,

Table 1. Self-reported highest educational degree obtained

Degree	DF, *N* (%)	HF, *N* (%)	HNF, *N* (%)	HNS, *N* (%)
GED/HS	6 (33.3)	3 (18.8)	2 (11.8)	4 (26.7)
Associates	1 (5.5)	5 (31.3)	1 (5.9)	2 (13.3)
Bachelors	6 (33.3)	6 (37.5)	7 (41.2)	6 (40)
Masters	4 (22.2)	2 (12.5)	5 (29.4)	3 (20)
Doctorate	1 (5.5)	0	2 (11.8)	0

DF = Deaf-Fluent, HF = Hearing-Fluent, HNF = Hearing Non-Fluent, HNS = Hearing Non-Signing.

Table 2. Sex, ASL-CT, and age of learning ASL by group

	DF	HF	HNF	HNS
Total *N* (female, male, other)	18 (9, 9, 0)	16 (10, 5, 1)	17 (15, 1, 1)	15 (10, 5, 0)
ASL-CT % correct mean (raw score)	87 (26)	80.2 (24)	57 (18)	-
Mean age when first learned sign language (SD)	2.2 (4.6)	13 (8.0)	24 (11.8)	-

ASL-CT = American Sign Language Comprehension Test, DF = Deaf-Fluent, HF = Hearing-Fluent, HNF = Hearing Non-Fluent, HNS = Hearing Non-Signing, SD = standard deviation.

Table 3. Self-reported educational history obtained for deaf fluent participants

School type	Elementary, *N* (%)	High school, *N* (%)	College, *N* (%)
Mainstream (no interpreter)	1 (5.6)	1 (5.6)	1 (5.6)
Mainstream (interpreter)	5 (27.8)	2 (11.1)	4 (22.2)
Deaf or Hard of Hearing program within mainstream school	4 (22.2)	3 (16.7)	1 (5.6)
Deaf school	8 (44.4)	12 (66.7)	12 (66.7)

parents' hearing status, and school type (i.e., mainstream or deaf school; see Table 3).

Our use of the term "fluency" throughout this paper is intended to convey the holistic amount of language knowledge, experience, and ease of comprehending and manipulating the language. We use this term broadly, for lack of a more encompassing term. There is no one point at which a person can be categorically deemed "fluent" using the ASL-CT, or any other ASL test available at the time of writing. Understanding a language (i.e., comprehension) also requires a different skillset than producing a language. For the current study, we opted to use the ASL-CT to determine a reasonable threshold for defining "fluency", although the test is one of comprehension (and not, for instance, sentence reproduction). We did so due to the published information about the percent correct and ASL-CT raw scores of hearing ASL students (63.3%, mean = 19 [3.4]), hearing native signers (72.0%, mean = 21.6 [5]), and deaf native signers (86.7%, mean = 26 [2]) which was used to create the a priori cutoffs for our participant groups.

EEG Stimuli

Stimuli used in this experiment are the same as those used in the original MRT developed by Shepard and Metzler (1971) and retrieved from http://wiki.cnbc.cmu.edu/Novel_Objects (SM-MRT; See Figure 1). We used 70 figure images from Shepard and Metzler's original stimulus library. We grouped stimuli into 280 pairs, fully crossing 10 figures, 2 trial types (same, different) and 10 angular disparities (0, ±20, ±40, ±60, ±80, ±100, ±120, ±140, ±160, ±180) in both the depth and plane characteristics. Due to previous work associating less mu desynchronization with increasing angular disparity (i.e., harder tasks), we also labeled all stimuli pairs as either differing in $< 100^\circ$ (i.e., easy) or $> 100^\circ$ (i.e., hard). We used 280 trials, a number comparable to other MRT studies that conducted similar EEG analyses (Chen et al., 2013; Gardony et al., 2017; Horster et al., 2013; Riecansky & Katina, 2010).

Procedure and Recording

Participants were fitted with an EEG cap and the researcher gave the instructions for the mental rotation task. A practice run was then completed. The practice section consisted of 10 unique stimuli pairs that are not in the real experiment. After the practice trials the experimenter answered any questions the participant had with the option of doing the practice trials again (no participants asked to repeat practice). Once the participant was comfortable with the instructions, we moved on to the real experiment.

The participant went through 280 total trials of the SM-MRT task, with breaks that were determined in length by the participant every 70 trials. The participant saw a fixation cross for 2000 ms, followed by 5,000 ms presentation of a stimuli pair. The response screen then appeared until the participant responded with either "SAME" or "DIFFERENT" by button press; this response screen was presented for a maximum of 3,000 ms. Button press responses also varied among participants, with half of the participants being instructed that "SAME" was indicated

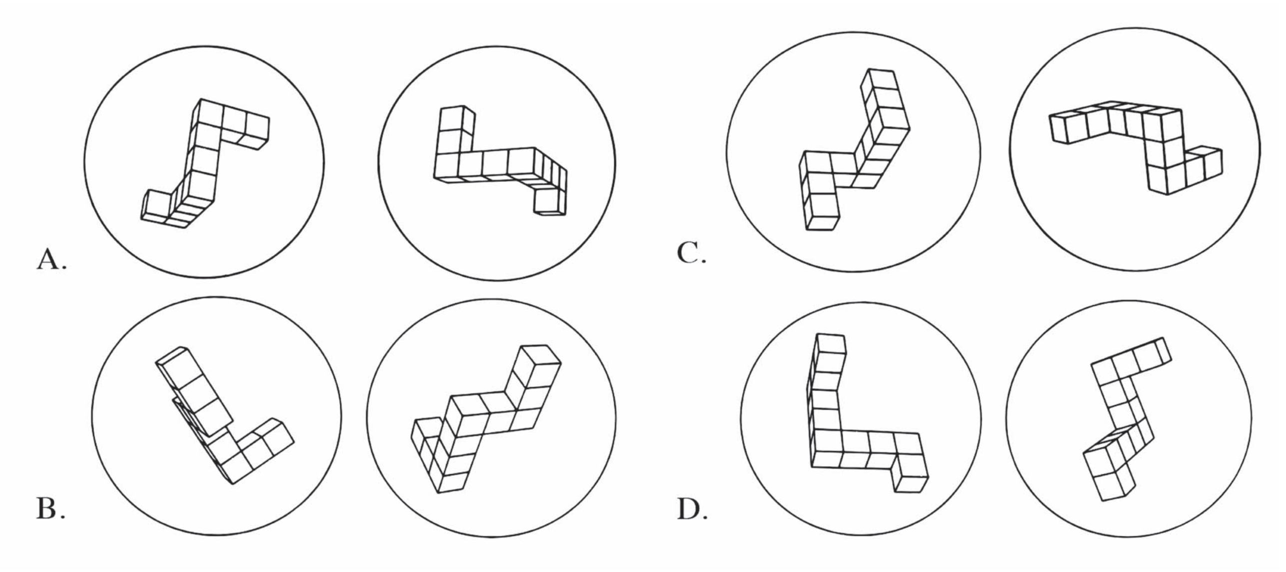

Figure 1. Example stimuli pairs from Mental Rotation Test. (A) Same-plane pair; these figures are the same object differed by 100° of rotation on the picture plane. (B) Same-depth pair; these figures are the same object differed by 100° of rotation on the vertical axis. (C) Different-plane pair; these are different objects (mirrored) rotated by 100° on the picture plane. (D) Different-depth pair; there are different objects (mirrored) rotated by 100° on the vertical axis.

by a left button press and "DIFFERENT" was indicated by a right button press, whereas the other half received the opposite instruction.

EEG was recorded from 64 active Ag/AgCl electrodes using an actiCAP setup (Brain Products GmbH, Germany), in combination with SuperVisc electrode gel. The EEG signals were amplified by the individual electrode amplifiers, and again by a 24-bit actiCHAMP amplifier (Brain Vision LLC, Morrisville, NC). The entire EEG portion of the experiment took around 45 min. When finished, participants received payment and were debriefed as to the main goals of the study. From start to finish, the experiment took about 2 hr.

EEG Data Preparation

All data processing was implemented using EEGLAB v. 14.1.2 (Delorme & Makeig, 2004). Data were referenced offline to the average of the two mastoid electrodes (TP9, TP10). Data were filtered offline using a .1 Hz high-pass and 100 Hz low-pass filter. Epochs were created from the continuous EEG, time-locked to stimuli (figure pairs). Onset of the stimulus was considered time 0, baseline was from −1,000 to 0, and epochs extracted from the continuous dataset included data from −500 to 2000 ms, including baseline and mental rotation related data. For the questions of interest in the present study, the time period from 0 to 1,500 ms was subjected to a time-frequency analysis. This analysis window is in line with prior EEG studies of mental rotation, due to the fact that the most evident EEG correlates of mental rotation occur within that window of time (Gardony et al., 2017; Horster et al., 2013; Milivojevic et al., 2011; Milivojevic et al., 2003).

Predictions

We predicted that the Fluent group (Deaf-Fluent and Hearing-Fluent) would perform better on mental rotation tasks than the Non-Skilled group (Hearing Non-Fluent and Hearing Non-Signers) due to previous work exploring the relationship between sign language fluency and visuospatial skills. Our second prediction was that the Deaf-Fluent group would perform better on mental rotation tasks than the Hearing-Fluent group due to the Deaf-Fluent group likely having more experience with ASL over a lifetime. There are no experimental paradigms to date that compare Deaf-Fluent signers against Hearing-Fluent signers in a classic MRT paradigm. Thus, our hypothesis is based on previous literature suggesting more practice with visuospatial abilities, in a variety of disciplines, can lead to transferable performance gains in said abilities (Overby, 1990; Ozel et al., 2002; Pérez-Fabello & Campos, 2007). As our third prediction, we predicted that the Fluent group (Deaf-Fluent, Hearing-Fluent) would show more sensorimotor system activity, as seen through mu desynchronization, compared with the Non-Skilled group (Hearing Non-Fluent, Hearing-Non-Signing) during mental rotation tasks due to differences in cognitive strategies. Our final prediction was that Deaf-Fluent signers would show more mu desynchronization compared with the Hearing-Fluent group during mental rotation tasks, suggesting more robust use of a motor simulation strategy. This prediction was based on previous work that found deaf signers outperform both hearing nonsigners and hearing signers in mental rotation and overall visuospatial abilities (Emmorey et al., 1998; McKee, 1987), suggesting varying neurobiological engagement (i.e., strategies) between groups.

Planned Analysis

Planned *t*-tests were driven by a priori predictions developed before data analysis (see above). In addition to the test described in detail below, tests also included analyses of VK-MRT accuracy between the Fluent and Non-Skilled and Deaf-Fluent and Hearing-Fluent groups to test for any significant differences ($p < .05$). Although we did collect responses from the SM-MRT during on-line EEG recording, we focused our analyses on the data from the VK-MRT because of its common use in the field and the fact that it avoids possible effects of attention over the duration of the EEG recording. To shed light on VK-MRT scores within each individual group, we conducted a one-way analysis of variance (ANOVA) with four levels and corrected for multiple comparisons (i.e., Deaf-Fluent, Hearing Fluent, Hearing Non-Fluent, Hearing Non-Signing). To assess if better or worse VK-MRT performance of any group is related to experiences with spatial activities, we conducted t-tests on scores from the SpES. We compared the Deaf-Fluent and Hearing-Fluent group scores as well as the overall Fluent and Non-Skilled groups.

Event-related spectral perturbations, which measure the changes in EEG power at different frequencies across time, were computed at each electrode within a central region of interest (ROI) (consisting of electrodes FC5, FC3, FC1, FCz, FC2, FC4, FC6, C5, C3, C1, Cz, C2, C4, C6, CP5, CP3, CP1, CPz, CP2, CP4, CP6; Delorme & Makeig, 2004) over the pre- and post-central gyrus. At each of these electrodes, we conducted *t*-tests (from −300 to 1,500 ms in time and 8–25 Hz in frequency, encompassing alpha and beta EEG frequencies) for all groups. We were particularly interested in significant effects seen at these electrodes because alpha and beta rhythms present at central electrodes are closely tied to activity in pre- and post-central gyri (primary motor and primary somatosensory cortices, respectively), areas strongly associated with motor simulation (Arnstein et al., 2011; Perry & Bentin, 2009; Ritter et al., 2009). For these ROI analyses, we used a p value of .05, with a false-discovery rate correction applied to control for false positives (Benjamini et al., 1995). We conducted t-tests comparing the Non-Skilled group to the Fluent group and the Deaf-Fluent group to the Hearing-Fluent group broken down by condition (i.e., easy and hard).

Results

Behavioral

All analyses were carried out in accord with the participant groupings described in the "participants" section. In accord with our planned analyses, we conducted t-tests of VK-MRT accuracy between Fluent and Non-Skilled groups and between the Deaf-Fluent and Hearing-Fluent groups. We found a significant difference ($t(64) = 2.42$, $p = .02$, $d = .60$; power = 15.5%) between Fluent and Non-Skilled groups' VK-MRT accuracies. We did not find significant differences when comparing the Deaf-Fluent and Hearing-Fluent VK-MRT accuracies ($t(32) = .95$, $p = .35$, $d = .33$; power = 67.5%; see Figure 2). We also found no statistically significant differences between individual group VK-MRT mean scores as determined by one-way ANOVA ($F(3, 62) = 2.22$, $p = .09$).

To assess if the better VK-MRT performance of the Fluent group compared with the Non-Skilled group was due to past spatial experiences, we conducted *t*-tests on scores from the SpES. The Fluent group did not have a significantly higher spatial experience score ($t(64) = .90$ $p = .34$, $d = .22$) than the Non-Skilled group. We also conducted *t*-tests between the Deaf-Fluent and Hearing-Fluent spatial experience scores and found that the Deaf-Fluent group had higher spatial experience scores than the Hearing-Fluent group ($t(25) = 3.01$, $p = .006$, $d = 1.02$). Because the Deaf-Fluent group and Hearing-Fluent groups scored similarly on the VK-MRT but the Deaf-Fluent group scored significantly higher in terms of overall spatial experience, we wanted to further investigate if involvement in spatial activities correlates with mental rotation abilities for signing populations. We found no significant correlation between spatial experience and mental rotation abilities for signing groups (Deaf-Fluent, Hearing-Fluent, Hearing Non-Fluent; $r(49) = .08$, $p = .56$). In addition to these analyses, we wanted to assess if the relationship between sign language comprehension and mental rotation abilities is continuous. To this end, we performed a partial correlation analysis between ASL-CT scores and VK-MRT scores while controlling for spatial experience. Participant scores from the Deaf-Fluent, Hearing-Fluent, and Hearing Non-Fluent groups were used ($n = 51$), as the Hearing-Non-Signing group did not take the ASL-CT (see Figure 3). We found a positive correlation between ASL-CT scores and VK-MRT scores ($r(50) = .47$, $p = .001$).

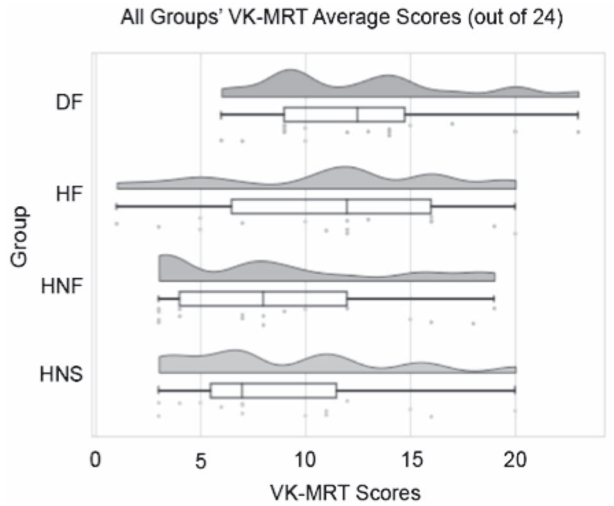

Figure 2. Raincloud plot showing Vandenberg and Kuse Mental Rotation Test scores by group. Group statistics and individual data points are both shown. DF = Deaf-Fluent, HF = Hearing Fluent, HNF = Hearing Non-Fluent, HNS = Hearing Non-Signers.

We analyzed the SM-MRT data, from the task concurrent with EEG recording, to help confirm that participants were completing the task as instructed. SM-MRT scores were raw number of correct trials, with a total possible score of 280. To parallel our analyses of the VK-MRT, we conducted t-tests of SM-MRT accuracy between Fluent and Non-Skilled groups and between the Deaf-Fluent and Hearing-Fluent groups. We found a significant difference ($p = .02$) between Fluent (M = 226.15, standard deviation [SD] = 23.10) and Non-Skilled (M = 211.28, SD = 28.78) groups' SM-MRT accuracies. We did not find significant differences when comparing the Deaf-Fluent (M = 222.11, SD = 22.12) and Hearing-Fluent (M = 230.69, SD = 24.04) SM-MRT accuracies ($t(32) = 1.08$, $p = .29$).

EEG

As this is the first study investigating neurobiological correlates of mental rotation in sign language users, we were interested in replicating the patterns in oscillatory EEG activity that have previously been associated with mental rotation. Similar to other studies with non-signers, our participants as a whole showed the typical ∼300 ms onset for desynchronization in alpha and beta frequency bands, indicating engagement of sensorimotor processing at that time (Chen et al., 2013; Gardony et al., 2017; Horster et al., 2013; Riecansky & Katina, 2010). Following this replication of prior work, we then created time-frequency plots to conduct *t*-tests comparing the Fluent group to the Non-Skilled group and comparing the Deaf-Fluent and Hearing-Fluent groups, both broken down further into "easy" and "hard" conditions. No electrodes within the

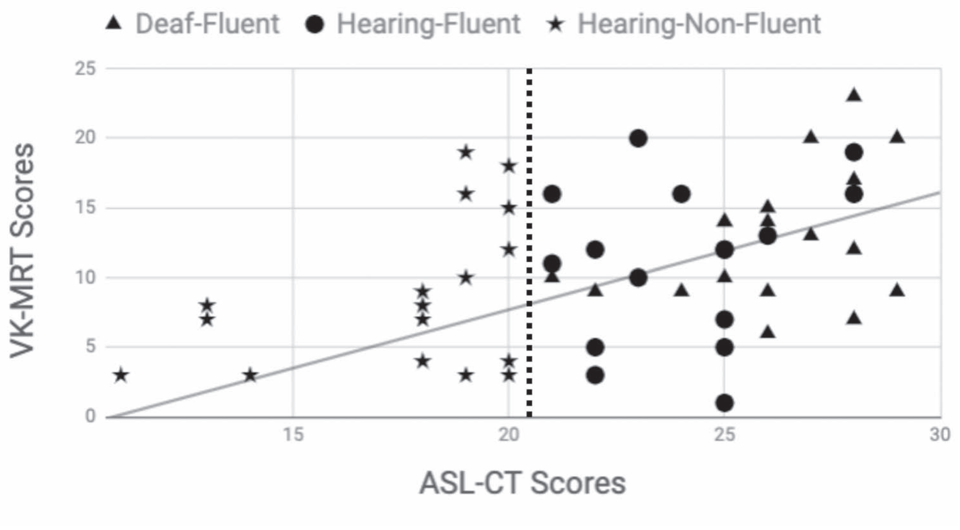

Figure 3. Scatterplot showing American Sign Language Comprehension Test (ASL-CT) scores and Vandenberg and Kuse Mental Rotation Test (VK-MRT) scores. The plot shows a positive relationship between VK-MRT and ASL-CT scores ($r(50) = .47$, $p = .001$). The dotted line indicates the cutoff for ASL fluency.

ROI showed significant differences in sensorimotor engagement as shown by alpha/beta power ($p < .05$, FDR corrected) for the Fluent versus Non-Skilled comparison or the Deaf-Fluent versus Hearing-Fluent comparison (see Figure 4). For all participants combined, there were no significant differences in alpha/beta power between easy and hard conditions.

Discussion

The goal of the current study was to investigate the neural and behavioral relationship between mental rotation abilities and sign language fluency. To that end, we designed a study exploring the use of different strategies during mental rotation tasks in individuals who possess various levels of sign language knowledge. Two of the main findings of the study are as follows: (1) Sign language comprehension and mental rotation abilities are positively correlated. (2) Behavioral performance differences between signers and non-signers are not clearly reflected in brain activity typically associated with mental rotation.

Fluent versus Non-skilled

Behavioral Our first aim was to compare the mental rotation abilities of a Fluent group (Deaf-Fluent, Hearing-Fluent) and a Non-Skilled group (Hearing Non-Fluent, Hearing-Non-Signing). We predicted that fluent signers will perform better on the VK-MRT, as seen through accuracy on the test, and this prediction was supported. Past work with mental rotation and signers has shown that signers, both deaf and hearing, show enhancement in mental rotation abilities compared with non-signers (Emmorey et al., 1998; Talbot & Haude, 1993). Our results not only support this notion, but add a group previously not studied under these conditions: hearing non-fluent signers. All but one previous study investigating the relationship between sign language and mental rotation only assess fluent signers and non-signers. Talbot and Haude (1993) gave mental rotation tasks to fluent signers, sign language students, and non-signers. However, both the ASL student group and the non-signers averaged less than 1 year of ASL experience, whereas the fluent group averaged 6 years. This vast discrepancy between group experiences does not allow questions to be answered related to the discrete or continuous relationship between sign language knowledge and mental rotation. Thus, for the first time in a study of mental rotation, we included a group of non-fluent signers to shed further light on the suggested mental rotation benefit possessed by sign language users.

To test if the relationship between mental rotation and sign language comprehension is discrete (i.e., only *fluent* sign language users show enhanced mental rotation abilities) or continuous (i.e., fluency is not necessary, your sign language comprehension score is related to mental rotation abilities regardless), we conducted a partial correlation analysis including all signing groups. We found a moderate positive correlation between sign language comprehension and mental rotation abilities. This means that as sign language comprehension increases, mental rotation abilities tend to increase as well. This is the first evidence suggesting that either (1) knowing some amount of sign language, even without fluency, can positively impact one's mental rotation abilities or (2) people who are better at learning ASL are those who are better at mental rotation. Previous studies make claims regarding the former, but only for those who are very experienced (i.e., fluent) in sign language compared with those who have no knowledge of the language whatsoever (Emmorey, 2001; McKee, 1987; Talbot & Haude, 1993). By including the Non-Fluent group here, we are able to see how a wide range of sign language knowledge relates to mental rotation abilities. The possibility remains that people who achieve higher fluency in ASL are people who are already better at mental rotation, perhaps due to an affinity for and a tendency to excel at spatial skills in general. Future work should aim to disentangle this relationship by conducting research that assesses mental rotation before and after sign language learning, to control for the effects of sign language directly.

Signers outperforming non-signers on measures of visuospatial ability has been seen many times over, showing fluent signers consistently outperforming non-signers on mental rotation tasks (Emmorey et al., 1998; Keehner & Gathercole, 2007; McKee, 1987; Talbot & Haude, 1993). However, a recent study suggests that deaf signers perform similarly to hearing non-signers on

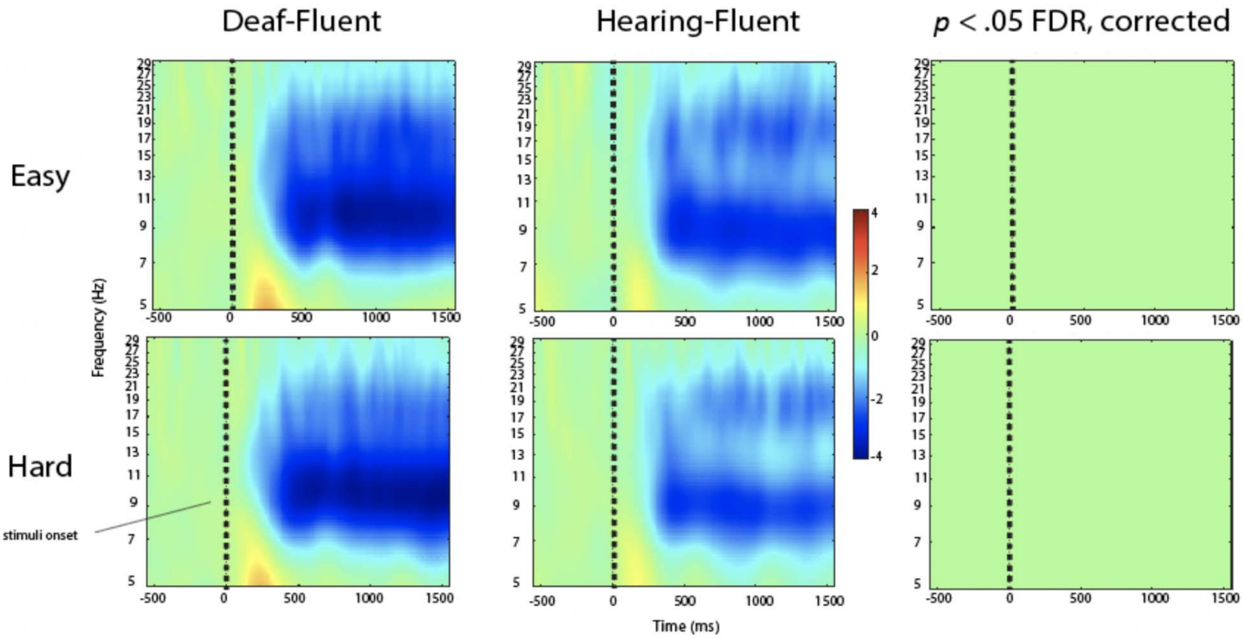

Figure 4. Alpha and beta power during Mental Rotation Test for deaf-fluent and hearing-fluent groups at electrode CP3. The top row shows differences between deaf-fluent and hearing-fluent groups in the easy condition. The bottom row shows differences between deaf-fluent and hearing-fluent groups in the hard condition. The third column shows that there are no significant differences ($p < .05$; FDR corrected) between the two groups in either condition. Electrode CP3 is reflective of results found for all other electrodes within the region of interest.

measures of mental rotation abilities (Secora & Emmorey, 2019), which is in contrast to the findings we present here. It is possible that differences in test administration explain this discrepancy. This recent paper administered the same measure of mental rotation abilities as we used here, with the same scoring system (VK-MRT; out of 24). The test provides instructions for how to proctor the test to participants, including word usage and timing. Secora et al. (2019) report that all participants were instructed to read the instructions, complete the practice items, and the test giver would provide clarifications as needed in ASL and/or spoken English. The deaf fluent signers in the current study and the Secora and Emmorey (2019) scored similarly on the VK-MRT (see Table 4). Differences in study results can be seen most notably in the hearing non-signing groups. Secora and Emmorey (2019) report participants in this non-signing group are “hearing college students.” In contrast, our hearing non-signing participants were recruited from the local community. It is possible that the hearing group in the Secora and Emmorey (2019) study are more practiced with visuospatial transformations than our community members due to their major and/or current classes, possibly explaining the higher than average mental rotation scores (see Table 4; Geiser et al., 2006; Pietsch & Jansen, 2012; Quaiser-Pohl & Lehmann, 2002; Quaiser-Pohl et al., 2005; Secora & Emmorey, 2019; Voyer, 1997).

One strength of the current study is that we ensured that all deaf participants received high quality signed instructions. We made this decision because it is possible that requesting deaf participants to read English can create intervening variables related to English reading skill level, which is not the focus of this study. Using only written instructions for a deaf signing group for a complex task of this type is not ideal because with a group comprised of primarily native signers, the issue of second language learning must be addressed. Although native or early exposure to sign language is more beneficial to English reading skills than late-exposure (Mayberry, 2007), English remains a second language for deaf native/early signers and should be treated as a confounding variable. Additionally, reading levels for deaf students, even college students, lag behind that of hearing peers (Moeller et al., 2007; Qi & Mitchell, 2011; Traxler, 2000). Thus, when adjusting tests for deaf signers, recommendations by test creators for verbal proctoring should not be replaced with independent reading, but with sign language proctoring.

A unique contribution of this study to the mental rotation and sign language literature is the consideration of prior spatial experience. Interestingly, although the Fluent group had higher mental rotation scores than the NonSkilled group, the Fluent group did not have higher spatial experience scores. Because past work has suggested that high scores on measures of visuospatial ability are likely due to past practice with highly spatial activities, we would expect that the Fluent group score higher than the NonSkilled group in spatial experience. However, this is not the case. The Fluent group and Non-Skilled group have similar spatial experiences, suggesting that the effect sign language fluency has on mental rotation abilities is more robust than any other spatial experience. When spatial experience is held constant, signers still perform better on measures of mental rotation due to their practice with a visuospatial language. This implies that sign language should be included in future measures of spatial experience, even if the focus of the study is not sign language use. For the first time, we provide evidence to support that those who are fluent in sign language, regardless of other spatial experiences, have enhanced visuospatial abilities that are transferable to measures of mental rotation performance.

EEG There is a current debate in the field of spatial cognition surrounding the topic of neural correlates during mental rotation tasks. There is literature suggesting there should be less mu desynchronization during mental rotation tasks if

Table 4. Means and standard deviation for Vandenberg and Kuse Mental Rotation Test in published work

Study	HNS male	HNS female	DF male	DF female	Total male	Total female	Total *N*
Voyer (1997)	14.12	9.24	-	-	155	207	362
Quaiser-Pohl and Lehmann (2002)	14.72 (4.6)	10.07 (4.4)	-	-	68	100	168
Quaiser-Pohl, Geiser, and Lehmann (2005)	11.69 (5)	8.67 (4.2)	-	-	356	505	861
Geiser, Lehmann, and Eid (2006)	13.02 (5.3)	9.2 (4.6)	-	-	843	850	1,693
Pietsch and Jansen (2012)	13.33 (.62*)	11.05 (.52*)	-	-	60	60	120
Secora and Emmorey (2019)	17 (6)	9 (4)	15 (6)	12 (6)	34	64	89
Secora and Emmorey (2020)	-	-	16 (5)	12 (6)	17	16	33
Current study	11.6 (5.9)	7.9 (4.4)	15 (4.5)	10.67 (4.2)	14	19	33

HNS = Hearing Non-Signing, DF = Deaf-Fluent.

skilled, and there is literature stating the opposite (Gardony et al., 2017; Horster et al., 2013). Although no study before this has investigated this topic through the lens of sign language users and we will thus yield novel insights, we also hope to shed light on the current debate surrounding the role of mu desynchronization during mental rotation tasks. We compared sensorimotor system activity during mental rotation tasks in the Fluent group (Deaf-Fluent, Hearing-Fluent) and the Non-Skilled group (Hearing Non-Fluent, Hearing Non-Signers). We predicted that fluent signers will show more mu desynchronization than other non-fluent groups during mental rotation tasks We hypothesized that extensive experience with ASL would translate into a greater ease of using a simulation-based strategy, and that this effect would be seen over the sensorimotor cortex (Gardony et al., 2017). However, although we did find behavioral differences between the Fluent and Non-Skilled groups, we did not see these differences reflected in the EEG analyses. More or less desynchronization in any group or condition would have shed light on the type of strategy used during mental rotation tasks (Gardony et al., 2017), thus clarifying the underlying mechanisms being used by fluent signers during mental rotation. These results do not support theories suggesting that those who are better at mental rotation utilize more motor simulation strategies (Gardony et al., 2017; Horster et al., 2013) or the opposing theory that suggests a type of neural efficiency is taking place for those more skilled at mental rotation, resulting in less desynchronization (Chen et al., 2013; Riecansky & Katina, 2010). Although recent evidence suggests signers are heavily practiced in mental rotation (either via motor simulation or analytical strategies), we found no evidence to demonstrate how this practice may impact neural processing outside of the non-linguistic domain of mental rotation. Paired with the behavioral data of the Fluent group outperforming the Non-Skilled group, these neurobiological correlates suggest processing of non-linguistic mental rotation may be taking place outside of canonical motor-related mental rotation areas. Our finding of no overall difference in alpha/beta EEG power between hard and easy conditions further supports the idea that any differences in how these trials are completed are not driven by differences in motor simulation.

Deaf-Fluent versus Hearing-Fluent

Behavioral We predicted that the deaf fluent group would show better performance on the VK-MRT than the Hearing-Fluent group due to greater long-term experience with sign language. Although the Deaf-Fluent group did score better than all other groups, there was no statistically significant difference between the Deaf-Fluent and Hearing-Fluent groups on the VK-MRT.

To investigate if spatial experiences impacted the comparison between Deaf-Fluent and Hearing-Fluent groups' mental rotation scores, we compared the two groups' spatial experience scores. Previous work suggests that performance on measures of mental rotation ability can be partially explained by experience with spatial activities. Thus, we would expect to see no significant difference between Deaf-Fluent and Hearing-Fluent groups. However, in our sample, the Deaf-Fluent group scored higher on spatial experience than the Hearing-Fluent group. We suggest that less involvement with spatial activities over a lifetime is not clearly related to mental rotation skills for sign language fluent populations, as the effect sign language fluency has on mental rotation abilities may be more robust than any other spatial experience. In this same line of reasoning, it is also possible that there is a ceiling effect with how much spatial experiences (i.e., soccer, drawing) can impact mental rotation abilities, thus suggesting the Deaf-Fluent group hit their ceiling with how much their mental rotation can be improved even with their significantly higher spatial experience scores.

EEG We aimed to further investigate cognitive strategies by examining the differences in sensorimotor system activity between Deaf-Fluent and Hearing-Fluent groups during both hard and easy mental rotation tasks. We predicted that the Deaf-Fluent group would show more mu desynchronization than the Hearing-Fluent group during mental rotation tasks, as the Deaf-Fluent group has more practice with mentally manipulating space over a lifetime, and thus would more readily use that cognitive strategy during mental rotation tasks. However, our time-frequency analysis results did not support this prediction. There was no statistically significant support for the idea that the Deaf-Fluent group and the Hearing-Fluent group would engage sensorimotor cortices differently during mental rotation tasks.

Although we did not find significant differences using our a priori statistical thresholds, we did notice consistent patterns in the data when examining the exact *p* values of the comparison between the groups. Across 16 of the 21 electrodes within our region of interest, we found there to be a reliable, yet not significant, pattern of more desynchronization for the Deaf-Fluent group compared with the Hearing-Fluent group in both alpha and beta band frequencies. A trend-level pattern of more mu desynchronization for the Deaf-Fluent group than the Hearing-Fluent group suggests the Deaf-Fluent group may in fact be calling upon motor simulation processes more robustly than the Hearing-Fluent group to solve these mental rotation tasks. However, it is possible that we do not see these differences either behaviorally or when statistical correction is applied because our group exclusion criteria is not strict enough to allow these effects to become fully apparent, resulting in a lack of power.

When looking at our a priori statistical analyses, particularly the time-frequency plots and scalp maps, the "hard" condition of the mental rotation task appears to recruit sensorimotor cortices similarly across both Deaf-Fluent and Hearing-Fluent groups, suggesting both groups are utilizing similar cognitive strategies (i.e., motor simulation, analytical) during hard mental rotation tasks. Although this finding makes sense, as the Deaf-Fluent and Hearing-Fluent groups did not score significantly different on the behavioral mental rotation test, we wanted to investigate the relationship between groups and condition further. Although our goal for the current study was to establish a foundation for further investigations into the neural correlates of spatial cognition in signers, and thus resulted in multiple groups across a range of ASL experiences, future work should aim to create larger sample sizes within each group (Fox et al., 2016) with more strict inclusion criteria to yield more distinct and clear results.

Future Directions and Conclusion

Although a positive correlation between spatial and success in STEM fields has been reliably substantiated over the past century, spatial thinking is still largely ignored in the vast majority of educational programs (Buckley et al., 2018; Newcombe, 2010; Super & Bachrach, 1957; Uttal et al., 2013b; Wai et al., 2009; Weisberg & Newcombe, 2017). In an effort to explore other possible avenues of STEM achievement, we investigated how sign language knowledge impacts mental rotation ability, a process foundational to spatial thinking. In this study, we aimed to further explore whether sign language comprehension affects visuospatial ability by investigating the behavioral and neurobiological relationship between sign language knowledge and mental rotation. This study addresses a gap in spatial cognition research by investigating groups with various levels of sign language knowledge to uncover interesting behavioral and neurobiological insights. We found that, similar to other studies, fluent signers outperform non-fluent and non-signers on measures of mental rotation. However, unlike previous studies, we were able to explore this relationship by using a test of sign language knowledge with a wide range of signers, revealing a positive correlation between mental rotation and sign language comprehension. Although it is possible that those are better at learning sign language are simply those who are better at mental rotation, it is also possible that knowledge of sign language, regardless of how much, can positively impact mental rotation abilities. This finding implies sign language can play an important role in embodied learning, specifically STEM learning. In an effort to shed further light on sign language's role in embodied learning, future work should aim to assess mental rotation before and after ASL learning to control for the effects of sign language.

We also found that, although fluent signers perform better than hearing non-fluent and hearing non-signers on mental rotation tasks, this difference is not clearly reflected in brain areas typically associated with mental rotation. Interestingly, whereas deaf fluent and hearing fluent signers performed similarly on mental rotation tasks, their brain activation showed different patterns of mu desynchronization for hard mental rotation tasks. Our results did not reach significance, but future work should aim for larger sample sizes for each group and more strict group exclusion criteria (i.e., native fluent only, non-native hearing only) to allow for robust effects of either early sign language exposure or deafness to come through more clearly. Overall, our work demonstrates the signing population's superior mental rotation abilities and establishes a basis for the investigation of neurobiological underpinnings of visuospatial skills in signing populations.

Conflicts of Interest

No conflicts of interest were reported.

Acknowledgments

The authors are grateful to Naseem Majrud and David Thornton for their contributions to this project. We are also thankful to Ilaria Berteletti, Deanna Gagne, and Nora Newcombe for their comments on a prior version of this work. We acknowledge the support of Gallaudet University, NSF/Gallaudet University's Science of Learning Center, VL2 (Visual Language and Visual Learning), and to Gallaudet University's Office of Research Support and International Affairs for the funds made available to complete this work.

References

Arnstein, D., Cui, F., Keysers, C., Maurits, N. M., & Gazzola, V. (2011). Mu-suppression during action observation and execution correlates with BOLD in dorsal premotor, inferior parietal and SI cortices. *Journal of Neuroscience*, *31*(40), 14243–14249. http://doi.org/10.1523/JNEUROSCI.0963-11.2011.

Bavelier, D., Brozinsky, C., Tomann, A., Mitchell, T., Neville, H., & Liu, G. (2001). Impact of early deafness and early exposure to sign language on the Cerebral Organization for Motion Processing. *The Journal of Neuroscience*, *21*(22), 8931–8942. https://doi.org/10.1523/jneurosci.21-22-08931.2001.

Benjamini, Y., Drai, D., Elmer, G., & Kafkafi, N. (1995). Controlling the false discovery rate in behavior genetics research. *Behavioural Brain Research*, *125*(1–2), 279–284.

Bowman, L. C., Bakermans-Kranenburg, M. J., Yoo, K. H., Cannon, E. N., Vanderwert, R. E., Ferrari, P. F., *et al.* (2017). The mu-rhythm can mirror: Insights from experimental design, and looking past the controversy. *96*, 121–125. http://doi.org/10.1016/j.cortex.2017.03.025.

Buckley, J., Seery, N., & Canty, D. (2018). A heuristic framework of spatial ability: A review and synthesis of spatial factor literature to support its translation into STEM education. *Educational Psychology Review*, *30*(3), 947–972. https://doi.org/10.1007/s10648-018-9432-z.

Chen, X., Bin, G., Daly, I., & Gao, X. (2013). Event-related desynchronization (ERD) in the alpha band during a hand mental rotation task. *Neuroscience Letters*, *541*, 238–242. http://doi.org/10.1016/j.neulet.2013.02.036.

Cherney, I. D., & Voyer, D. (2009). Development of a spatial activity questionnaire I: Items identification. *Sex Roles*, *62*, 89–99. http://doi.org/10.1007/s11199-009-9710-9.

Corina, D. P., & Knapp, H. (2006). Sign language processing and the mirror neuron system. *Cortex*, *42*(4), 529–539. http://doi.org/10.1016/S0010-9452(08)70393-9

Corina, D., Chiu, Y.-S., Knapp, H., Greenwald, R., San Jose-Robertson, L., & Braun, A. (2007). Neural correlates of human action observation in hearing and deaf subjects. *Brain Research*, *1152*, 111–129. http://doi.org/10.1016/j.brainres.2007.03.054.

Debnath, R., Salo, V. C., Buzzell, G. A., Yoo, K. H., & Fox, N. A. (2019). Mu rhythm desynchronization is specific to action execution and observation: Evidence from time-frequency and connectivity analysis. *NeuroImage*, *184*, 496–507. http://doi.org/10.1016/j.neuroimage.2018.09.053.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009.

Dror, I. E., Kosslyn, S. M., & Waag, W. L. (1993). Visual-spatial abilities of pilots. *Journal of Applied Psychology*, *78*(5), 763–773. http://doi.org/10.1037/0021-9010.78.5.763.

Emmorey, K. (2001). *Language, cognition, and the brain: Insights from sign language research*. The Salk Institute for Biological Studies, Psychological Press. https://doi.org/10.4324/9781410603982

Emmorey, K., Damasio, H., McCullough, S., Grabowski, T., Ponto, L. L. B., Hichwa, R. D., *et al.* (2002). Neural systems underlying spatial language in American sign language. *NeuroImage*, *17*(2), 812–824. http://doi.org/10.1006/nimg.2002.1187.

Emmorey, K., Grabowski, T., McCullough, S., Ponto, L. L. B., Hichwa, R. D., & Damasio, H. (2005). The neural correlates of spatial language in English and American sign language: A PET study with hearing bilinguals. *NeuroImage*, *24*(3), 832–840. https://doi.org/10.1016/j.neuroimage.2004.10.008.

Emmorey, K., Klima, E., & Hickok, G. (1998). Mental rotation within linguistic and non-linguistic domains in users of American Sign Language. *Cognition*, *68*(3), 221–246.

Emmorey, K., Kosslyn, S. M., & Bellugi, U. (1993). Visual imagery and visual-spatial language: Enhanced imagery abilities in deaf and hearing ASL signers. *Cognition*, *46*(2), 139–181.

Emmorey, K., Mehta, S., McCullough, S., & Grabowski, T. G. (2016). The neural circuits recruited for the production of signs and fingerspelled words. *Brain and Language*, *160*, 30–41. https://doi.org/10.1016/j.bandl.2016.07.003.

Estes, Z., & Felker, S. (2011). Confidence mediates the sex difference in mental rotation performance. *Archives of Sexual Behavior*, *41*(3), 557–570. http://doi.org/10.1007/s10508-011-9875-5.

Fox, N. A., Bakermans-Kranenburg, M. J., Yoo, K. H., Bowman, L. C., Cannon, E. N., Vanderwert, R. E., *et al.* (2016). Assessing human mirror activity with EEG mu rhythm: A meta-analysis. *Psychological Bulletin*, *142*(3), 291. https://doi.org/10.1037/bul0000031.

Gardony, A. L., Eddy, M. D., Brunyé, T. T., & Taylor, H. A. (2017). Cognitive strategies in the mental rotation task revealed by EEG spectral power. *Brain and Cognition*, *118*, 1–18. http://doi.org/10.1016/j.bandc.2017.07.003.

Geiser, C., Lehmann, W., & Eid, M. (2006). Separating "rotators" from 'nonrotators' in the mental rotations test: A multigroup latent class analysis. *Multivariate Behavioral Research*, *41*(3), 261–293. https://doi.org/10.1207/s15327906mbr4103_2.

Hauser, P. C., Paludneviciene, R., Riddle,W., Kurz, K. B., Emmorey, K., & Contreras, J. (2015). American sign language comprehension test: A tool for sign language researchers. Journal of Deaf Studies and Deaf Education, 21(1), 64–69. https://doi.org/10.1093/deafed/env051

Horster, A. C., van Lier, R., & Steenbergen, B. (2013). Mental rotation strategies reflected in event-related (de)synchronization of alpha and mu power. *Psychophysiology*, 50(9), 858–863. http://doi.org/10.1111/psyp.12076.

Keehner, M., & Gathercole, S. E. (2007). Cognitive adaptations arising from nonnative experience of sign language in hearing adults. *Memory & Cognition*, 35(4), 752–761. https://doi.org/10.3758/bf03193312.

Mayberry, R. (2007). When timing is everything: Age of first-language acquisition effects on second-language learning. *Applied Psycholinguistics*, *28*(03). https://doi.org/10.1017/s0142716407070294.

McKee, D. (1987). An analysis of specialized cognitive functions in deaf and hearing signers, 1–186. (Doctoral Dissertation).

Meade, G., Midgley, K. J., Sehyr, Z. S., Holcomb, P. J., & Emmorey, K. (2017). Implicit co-activation of American sign language in deaf readers. *An ERP study*, *170*, 50–61. http://doi.org/10.1016/j.bandl.2017.03.004.

Milivojevic, B., Hamm, J. P., & Corballis, M. C. (2011). About turn: How object orientation affects categorisation and mental rotation. *Neuropsychologia*, *49*(13), 3758–3767. http://doi.org/10.1016/j.neuropsychologia.2011.09.034.

Milivojevic, B., Johnson, B. W., Hamm, J. P., & Corballis, M. C. (2003). Non-identical neural mechanisms for two types of mental transformation: Event-related potentials during mental rotation and mental paper folding. *Neuropsychologia*, *41*(10), 1345–1356. https://doi.org/10.1016/s0028-3932(03)00060-5.

Moeller, M. P., Tomlin, J. B., Yoshinaga-Itano, C., Connor, C. M., & Jerger, S. (2007). Current state of knowledge: Language and literacy of children with hearing impairment. *Ear Hearing*, *28*(6), 740–753. https://doi.org/10.1097/aud.0b013e318157f07f.

Morford, J. P., Wilkinson, E., Villwock, A., Piñar, P., & Kroll, J. F. (2011). When deaf signers read English: Do written words activate their sign translations? *Cognition*, *118*(2), 286–292. http://doi.org/10.1016/j.cognition.2010.11.006.

Muthukumaraswamy, S. D., Johnson, B. W., & McNair, N. A. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195–201. http://doi.org/10.1016/j.cogbrainres.2003.12.001.

Newcombe. (2010). Picture this: Increasing math and science learning by improving spatial thinking. *American Educator*. http://doi.org/10.1037/a0016127.

Newcombe, & Shipley. (2014). Thinking About Spatial Thinking: New Typology, New Assessments. In *Studying Visual and Spatial Reasoning for Design Creativity* (pp. 179–192). Springer Netherlands. http://doi.org/10.1007/978-94-017-9297-4_10.

Newcombe, Bandura, & Taylor (1983). Sex differences in spatial ability and spatial activities. *Sex Roles*, *9*(3), 377–386. http://doi.org/10.1007/BF00289672.

Oberman, L. M., McCleery, J. P., Ramachandran, V. S., & Pineda, J. A. (2007). EEG evidence for mirror neuron activity during the observation of human and robot actions: Toward an analysis of the human qualities of interactive robots. *Neurocomputing*, *70*(13–15), 2194–2203. http://doi.org/10.1016/j.neucom.2006.02.024.

Overby, L. Y. (1990). A comparison of novice and experienced dancers' imagery ability. *Journal of Mental Imagery*, *14*(3–4), 173–184.

Ozel, S., Larue, J., & Molinaro, C. (2002). Relation between sport activity and mental rotation: Comparison of three groups of subjects. *Perceptual and Motor Skills*, 95, 1141–1154. https://doi.org/10.2466/pms.2002.95.3f.1141.

Parasnis, I., Samar, V. J., Bettger, J. G., & Sathe, K. (1996). Does deafness lead to enhancement of visual spatial cognition in children? Negative evidence from deaf nonsigners. *Journal of Deaf Studies and Deaf Education*, *1*(2), 145–152.

Perry, A., & Bentin, S. (2009). Mirror activity in the human brain while observing hand movements: A comparison between

EEG desynchronization in the μ-range and previous fMRI results. *Brain Research*, *1282*, 126–132. http://doi.org/10.1016/j.brainres.2009.05.059.

Peters, M., Laeng, B., Latham, K., Jackson, M., Zaiyouna, R., & Richardson, C. (1995). A redrawn Vandenberg and Kuse Mental Rotations Test-different versions and factors that affect performance. *Brain and Cognition*, *38*, 39–58.

Petitto, L. A., Zatorre, R. J., Gauna, K., Nikelski, E. J., Dostie, D., & Evans, A. C. (2000). Speech-like cerebral activity in profoundly deaf people processing signed languages: Implications for the neural basis of human language. *97*(25), 13961–13966. http://doi.org/10.1073/pnas.97.25.13961.

Pérez-Fabello, M. J., & Campos, A. (2007). Influence of training in artistic skills on mental imaging capacity. *Creativity Research Journal*, *19*(2–3), 227–232. http://doi.org/10.1080/10400410701397495.

Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *NeuroImage*, *31*(1), 153–159. http://doi.org/10.1016/j.neuroimage.2005.12.003.

Pietsch, S., & Jansen, P. (2012). Different mental rotation performance in students of music, sport and education. *Learning and Individual Differences*, *22*(1), 159–163. http://doi.org/10.1016/j.lindif.2011.11.012.

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating “seeing” and “hearing” into doing. *Brain Research Reviews*, 50(1), 57–68. http://doi.org/10.1016/j.brainresrev.2005.04.005.

Pyers, J. E., Shusterman, A., Senghas, A., Spelke, E., & Emmorey, K. (2010). Evidence from an emerging sign language reveals that language supports spatial cognition. *Pnas*, *107*(27), 12116–12120. http://doi.org/10.1073/pnas.0914044107.

Qi, S., & Mitchell, R. E. (2011). Large-scale academic achievement testing of deaf and hard-of-hearing students: Past, present, and future. *Journal of Deaf Studies and Deaf Education*, *17*(1), 1–18. http://doi.org/10.1093/deafed/enr028.

Quaiser-Pohl, C., & Lehmann, W. (2002). Girls’ spatial abilities: Charting the contributions of experiences and attitudes in different academic groups. *British Journal of Educational Psychology*, *73*, 245–260. https://doi.org/10.1348/000709902158874

Quaiser-Pohl, C., Geiser, C., & Lehmann, W. (2005). The relationship between computer-game preference, gender, and mental-rotation ability. *Personality and Individual Differences*, *40*(3), 609–619. http://doi.org/10.1016/j.paid.2005.07.015.

Quandt, L. C., & Kubicek, E. (2018). Sensorimotor characteristics of sign translations modulate EEG when deaf signers read English. *Brain and Language*, *187*, 9–17. http://doi.org/10.1016/j.bandl.2018.10.001.

Quandt, L. C., & Marshall, P. J. (2014). The effect of action experience on sensorimotor EEG rhythms during action observation. *Neuropsychologia*, *56*, 401–408. http://doi.org/10.1016/j.neuropsychologia.2014.02.015.

Riecansky, I., & Katina, S. (2010). Induced EEG alpha oscillations are related to mental rotation ability: The evidence for neural efficiency and serial processing. *Neuroscience Letters*, *482*(2), 133–136. http://doi.org/10.1016/j.neulet.2010.07.017.

Ritter, P., Moosmann, M., & Villringer, A. (2009). Rolandic alpha and beta EEG rhythms’ strengths are inversely related to fMRI-BOLD signal in primary somatosensory and motor cortex. *Human Brain Mapping*, *30*(4), 1168–1187. http://doi.org/10.1002/hbm.20585.

Secora, K., & Emmorey, K. (2019). Social abilities and visual-spatial perspective-taking skill: Deaf signers and hearing nonsigners. *Journal of Deaf Studies and Deaf Education*, *24*(3), 201–213. http://doi.org/10.1093/deafed/enz006.

Secora, K., & Emmorey, K. (2020). Visual perspective-taking in spatial scenes and in American sign language. *Journal of Deaf Studies and Deaf Education*.

Sorby, S. (1999). Developing 3D spatial visualization skills. *Engineering Design Graphics Journal*, *63*(2), 21–32.

Super, D., & Bachrach, P. (1957). *Scientific careers and vocational development theory: A review, a critique, and some recommendations*. Teachers Coll. Press.

Talbot, K. F., & Haude, R. (1993). The relation between sign language skill and spatial visualization ability: Mental rotation of three-dimensional objects. *Perceptual and Motor Skills*, *77*, 1387–1391.

Terlecki, M. S., & Newcombe (2005). How important is the digital divide? The relation of computer and videogame usage to gender differences in mental rotation ability. *Sex Roles*, *53*(5–6), 433–441. http://doi.org/10.1007/s11199-005-6765-0.

Traxler, C. B. (2000). The Stanford achievement test, 9th edition: National Norming and performance standards for deaf and hard-of- hearing students. *Journal of Deaf Studies and Deaf Education*, *5*(4), 1–12. https://doi.org/10.1093/deafed/5.4.337.

Ulloa, E., & Pineda, J. (2007). Recognition of point-light biological motion: Mu rhythms and mirror neuron activity. *183*(2), 188–194. http://doi.org/10.1016/j.bbr.2007.06.007.

Uttal, D. H., Meadow, N. G., Tipton, E., Hand, L. L., Alden, A. R., Warren, C., *et al.* (2013a). The malleability of spatial skills: A meta-analysis of training studies. *Psychological Bulletin*, *139*(2), 352–402. http://doi.org/10.1037/a0028446.

Uttal, D. H., Miller, D. I., & Newcombe (2013b). Exploring and enhancing spatial thinking. *Current Directions in Psychological Science*, *22*(5), 367–373. http://doi.org/10.1177/0963721413484756.

Voyer, D. (1997). Scoring procedure, performance factors, and magnitude of sex differences in spatial performance. *American Journal of Psychology*, *110*(2), 259.

Wai, J., Lubinski, D., & Benbow, C. P. (2009). Spatial ability for STEM domains: Aligning over 50 years of cumulative psychological knowledge solidifies its importance. *Journal of Educational Psychology*, *101*(4), 817–835. http://doi.org/10.1037/a0016127.

Weisberg, S. M., & Newcombe, N. S. (2017). Embodied cognition and STEM learning: Overview of a topical collection in CR:PI. *Cognitive Research*, *2*, 38. http://doi.org/10.1186/s41235-017-0071-6.

Zacks, J. M. (2008). Neuroimaging studies of mental rotation: A meta-analysis and review. *Journal of Cognitive Neuroscience*, *20*(1), 1–19. https://doi.org/10.1162/jocn.2008.20013.