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Telling Right from Right: The Influence of Handedness in the Mental Rotation of Hands

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Telling Right from Right: The Influence of Handedness in the Mental Rotation of Hands

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by

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Abstract

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by

You Cheng

In mental rotation tasks (MRT), people show a remarkably different pattern of responses to hand stimuli compared to geometric 3D objects. However, the mechanisms of these effects remain unclear. In order to provide a more solid understanding of the cognitive processes involved in the mental rotation of hands, I tested both left-handed and right-handed subjects on a modified Shepard & Metzler task with hand stimuli. I crossed two orthogonal hypothesis axes to yield four competing hypotheses. One axis of the hypothesis space contrasted i) embodied experience (people's experience with their own hands) versus ii) world knowledge of a right-handed world. The other hypothesis axis contrasted a) the holistic motor imagery matching between the visual image of a hand on the screen and one's own hand versus b) the resemblance of only the shape outline information from the hand stimuli with the proprioception of one's own hands. The results suggest that, for mixed-handed people, embodied experience is important in the mental rotation of hands and the information is likely processed through a visual-proprioceptive integration cognitive mechanism. However, for extreme-handed people, the results only showed that extreme right-handers had overall better performance than extreme left-handers. World knowledge might independently influence performance for left hand stimuli while the performance for right hand stimuli is influenced by a combination of world knowledge and embodied

experience. Finally, I discuss potential future studies that could further test embodied experience versus world knowledge in left-handed and right-handed people.

Introduction

The goal of the mental rotation task is to determine whether two images shown from different viewpoints portray the same object. Researchers are interested in this task because it shows an elegant result in which reaction time linearly increases with rotational angle, suggesting that spatial processes have important roles to play in thinking. The mental rotation of hands is a specific subtype of the mental rotation task in which the participants must determine whether 2-dimensional hand pictures are the same (e.g., both are left hands, or both are right hands) or different hands (e.g., are a left hand and a right hand). In the mental rotation of hands, response time is much faster and more invariant to changes in orientation than for the mental rotation of other objects (Cooper, 1975; Cooper & Shepard, 1975; Folk & Luce, 1987; Shepard & Metzler, 1971; Stieff, 2007). The goal of the current study is to explore the cognitive mechanisms underlying this unusual effect using palm-up hand stimuli. In the introduction to this thesis, I will first review the literature on the mental rotation of hands and then introduce the main factors (handedness direction, handedness strength, embodied experience, and world knowledge) considered in the thesis experiment.

Hand Mental Rotation Tasks

Before introducing specific tasks, it is worth mentioning that most previous hand mental rotation tasks either only used palm-down stimuli or used a mixture of palm-up and palm-down stimuli. I will specify the hand stimuli used in the task when I describe previous studies below.

Two primary tasks have been developed to study the mental rotation of hands. One task is the hand laterality task, meaning the person must determine whether the hand is a left hand or a right hand. In this task, subjects are presented with one hand at a time and need to judge its laterality by pressing the 'left' or 'right' button. The second type of task is a modified Shepard and Metzler task (SMT), in which subjects are presented with two hands simultaneously, one on each side of the screen. The task is to decide whether the two hands are the same hand (both are left hands or both right hands) or different (one is a left hand, one is a right hand). The hand laterality task is used more often to study motor behavior (e.g. Parsons, 1994), while the hand version of the SMT is more commonly tested together with SMT of other stimuli (e.g. tools, letters, cubes) to illustrate the striking difference in performance for hands. Although both tasks show a flat response function between hand orientation and reaction time, indicating an invariant response compared to other mental rotation tasks (Cooper, 1975; Cooper & Shepard, 1975; Folk & Luce, 1987; Shepard & Metzler, 1971; Stieff, 2007), I prefer the SMT version for four reasons. First, at the verbal labelling stage of the hand laterality task, the left-right judgment potentially leads to confusion in telling left from right, which could interfere with testing mental rotation ability. This left-right confusion is quite common in human population, even in highly educated groups (Harris, 1972), which could complicate the interpretation of responses. Second, a previous study showed that the subjective frame of reference in the hand laterality task is influenced by head tilt (Sekiyama, 1982). Therefore, unless each subject's head position is monitored during the experiment, results of the hand laterality task could be noisy due to head motion. In the SMT, however, the subjective frame of reference is not required to define orientation of stimuli. Instead, the orientation is defined by the relative position between two presented stimuli in each trial, so performance is more invariant to the subjects' own position. This dissociation is also supported by existing research on mental rotation of body images that compared the SMT and hand laterality task (Zacks, Mires, Tversky, & Hazeltine, 2002). The study suggests that the laterality task recruits egocentric perspective transformations in which spatial information is formed with respect to oneself, while the body version of SMT recruits object-based spatial transformations in which spatial information is formed independent of the observer's view.

Third, it is possible that because the hand laterality task recruits egocentric perspective transformations, subjects are more likely to simulate the hand stimulus on the screen with their own hand by imagining rotating their own hand to complete the task. On the one hand, this imagining confounds whether the involvement of motor cortex derives from the process of completing the hand mental rotation task itself or a strategy to solve the task at the conscious level. On the other hand, when viewed from the egocentric perspective, this imaged rotation could lead to poorer performance in the hand laterality task for hand orientations that are not within normal ranges of hand motion. Some of the earliest evidence for biomechanical limitations comes from Parsons (1987), which will be described in detail below when introducing "motor simulation theory". Fourth, the formerly-mentioned verbal labelling of left/right in the hand laterality task potentially facilitates subjects' using their own left and right hand as a reference for making left/right judgements, thus becoming more susceptible to errors for orientations that fall out of normal hand motion ranges.

Embodied Experience and World Knowledge

Two theories largely drive contemporary understanding of the influence of handedness in the mental rotation of hands. They are key because they inform how research on the topic should be designed.

Embodied experience theory. Hands, as parts of the human body, provide us with embodied experience through our interaction with the world. The hand that is used more often in daily life – the dominant hand – typically provides more embodied experience. Therefore, people are likely to have greater embodied experience with their dominant hand than with their non-dominant hand. For example, a study on the hand laterality task (2 stimuli in palm-up position, 2 stimuli in palm-down position) in upper limb amputees found that subjects who lost their dominant limb showed less accuracy and longer latency than subjects who lost their non-dominant limb (Nico, Daprati, Rigal, Parsons, & Sirigu, 2004). This study suggests the importance of embodied experience from (dominant) hands in the mental rotation of hands.

World knowledge theory. As approximately 90% of human beings are right-handed, defined either by skill or preference in spite of culture or ethnicity (Coren & Porac, 1977; Previc, 1991), almost all tools and facilities (e.g. scissors, notebooks, spiral staircases) in daily life are designed for right-handed people. In other words, we live in a right-handed world. A study on left- and right-handed split-brain patients revealed that the right hand, regardless of hand dominance, has an advantage in representing acquired tool-use skills (e.g. pantomime actions associated with tools); based on the prior knowledge that the left hemisphere controls the right hand, this finding suggests that tool use is related to left hemisphere (Frey, Funnell, Gerry, & Gazzaniga, 2005). Therefore, the possibility exists that everyone is more familiar with right hands than left hands, regardless of handedness, because we live in a right-handed world.

Based on the previous considerations, both embodied experience and world knowledge could explain people's familiarity with right or left hands, and further could be considered as a factor underlying the mental rotation of hands. A good way to test these two theories is by contrasting performance between left-handers and right-handers. If the mental rotation of hands is supported by world knowledge, then everyone will be more familiar with right hands than with left hands. Under this theory, I predict that all people will perform better on right hand stimuli than on left hand stimuli, independent of handedness. In contrast, if the mental rotation of hands is supported by embodied experience, an advantage for the dominant hand is expected. Thus, left-handers are predicted to have better performance for left hand stimuli, and right-handers will have better performance for right hand stimuli. Next, I provide a literature review on handedness research in order to have a thorough consideration of the influence of handedness.

Handedness

Direction of handedness. Handedness has been studied since the 17th century (Browne, 1964). It is one of the most fundamental personal characteristics in that it is a universal trait that is both inherited and is not as socially variable in its manifestation compared with other complex characteristics (e.g., language, religion, intelligence, etc.). Thus, it is a salient variable that can possibly be considered to assess behavioral connections at an unconscious level. Numerous factors related to handedness have been determined. Besides the unbalanced distribution of left-handers and right-handers in the human population, an unbalanced gender distribution is also found in each handedness group: a higher proportion of males (e.g., 10.6% in the 1994 study) are left-handed than females (e.g., 8.5% in the 1994 study) (Annett, 1973; Perelle & Ehrman, 1994). This gender difference explains why it is challenging for laterality studies to recruit equal numbers of males and females in their left-handed and right-handed groups. As for the determinants of one's handedness, intriguing discoveries provide evidence that handedness is determined prenatally, such as differences in left and right hand growth rate surfacing during hand development at week 7 of the embryo stage (O'rahilly & Müller, 2010) and thumb sucking behavior at week 15 of the fetus stage (Hepper, Shahidullah, & White, 1991; Hepper, Wells, & Lynch, 2005). As for a genetic influence, statistical analysis of the relationship between one's own handedness and the handedness of parents, children, and siblings has revealed conflicting results, but overall indicates that handedness within families is determined more by social factors than by genetics (Perelle & Ehrman, 1994; Searleman, Herrmann, & Coventry, 1984). Therefore, it is more conservative to regard 'handedness' as a form of embodied experience that draws from both nature and nurture, as opposed to having a purely genetic or social basis.

Whether one is left- or right-handed could have an impact on cognitive skills. Previous studies on cognitive abilities between left-handers and right-handers indicate inconsistent results on most cognitive tasks, including intelligence (Benbow, 1986; Gregory & Paul, 1980; Papadatou-Pastou & Tomprou, 2015; Pirozzolo & Rayner, 1979), anxiety (Hicks & Pellegrini, 1978; Wienrich, Wells, & McManus, 1982; Wright & Hardie, 2012), illness (Bakan, 1971; Bakan, Dibb, & Reed, 1973; Geschwind & Galaburda, 1985; Lauren J Harris, 1993; Lauren Julius Harris & Carlson, 1988), verbal abilities (Kocel, 1977; Miller, 1971; Natsopoulos, Kiosseoglou, Xeromeritou, & Alevriadou, 1998; Sherman, 1979), and spatial abilities (Annett, 1992; Eme, Stone, & Izral, 1978; Gilbert, 1977; Kocel, 1977; Reio, Czarnolewski, & Eliot, 2004). Meta-analyses of handedness and cognitive abilities literatures show no difference in intelligence between right- and left-handers (Ntolka & Papadatou-Pastou, 2018) and, interestingly, found a significant advantage for right-handers only in mental rotation tasks (Somers, Shields, Boks, Kahn, & Sommer, 2015), which indicates that embodied hand experience could affect mental rotation performance. Although handedness does not influence attention (Śmigasiewicz, Liebrand, Landmesser, & Verleger, 2017), researchers observed that brain regions involved in the attentional network are more right-lateralized in right-handers than in left-handers (Liu, Stufflebeam, Sepulcre, Hedden, & Buckner, 2009). These asymmetrical attentional networks indicate a potential role of visual perception processes.

Strength of handedness. In addition to studying the direction of handedness (i.e., left or right), another thread of research focuses on the strength of handedness. The strength of handedness varies from mixed (inconsistent hand preference for activities) to extreme (very consistent in using either the left or the right hand). Because the movement of one hand is contralaterally regulated by the other brain hemisphere, researchers have hypothesized that extreme-handed individuals have less interhemispheric interaction than mixed-handed individuals (Christman, Propper, & Dion, 2004). This hypothesis is supported by evidence that left and right extreme-handed individuals have less cognitive flexibility than mixed-handed individuals. For example, extreme-handed individuals are less likely to endorse unconventional beliefs (Badzakova-Trajkov, Häberling, & Corballis, 2011; Barnett & Corballis, 2002; Nicholls, Orr, & Lindell, 2005), are worse in tasks involving counterfactual thinking (Jasper, Barry, & Christman, 2008), and are more authoritarian in political attitude (Grillo, Pupcenoks, & Lyle, 2018; Lyle & Grillo, 2014). Since there are not many extreme left-handers, sometimes studies only compare extreme right-handers with left and right mixed-handers. For example, extreme right-handers are less willing to update their beliefs and attitudes even facing persuasive information (Christman, Henning, Geers, Propper, & Niebauer, 2008), are less willing to engage in games that they perceive to be risky (Christman, Jasper, Sontam, & Cooil, 2007), and are also less likely to prefer unconventional music genres (Christman, 2013). Neuroimaging studies also indicate that part of the corpus callosum, the main pathway for interhemispheric interaction, may be smaller for extreme-handed individuals (Cowell, Kertesz, & Denenberg, 1993; Habib et al., 1991). It is possible that mixed-handed people tend to be more flexible in using strategies in the mental rotation of hands than extreme-handed people.

The strength of handedness may also be an important individual difference factor in episodic memory: extreme right-handers have lower memory accuracy (Propper & Christman, 2004) and perform worse on memory tasks which require hemispheric interaction (e.g. paired associate recall) (Lyle, McCabe, & Roediger, 2008; Lyle & Orsborn, 2011; Propper, Christman, & Phaneuf, 2005); extreme-handed individuals have worse memory for unimanual hand use (Edlin, Carris, & Lyle, 2013). However, when asking subjects to make saccadic eye movements toward visual targets immediately before the retrieval phase, saccades only improved memory retrieval of extreme-handed individuals while they barely improved memory for mixed-handed groups (Lyle, Hanaver-Torrez, Hackländer, & Edlin, 2011; Lyle, Logan, & Roediger, 2008).

Even though sometimes researchers combine extreme left-handers with left and right mixed handers into one group to compare with extreme right-handers, due to the small population of extreme left-handers, the average absolute handedness strength of the mixed group was always lower than the pure extreme right-handed group. There is a possibility that what really matters is the handedness strength per se instead of whether the subject is an extreme right-hander. Thus, I included extreme left-handers (although the sample size is also fairly small) in the extreme-handed group for data analysis, aiming to take a closer look at the influence of handedness strength. Because extreme-handers will have more embodied experience with their dominant hands than mixed-handers, I expect subjects' performance for right hand stimuli will increase from extreme left-hander to mixed left-hander to mixed right-hander to extreme right hander, and performance for left hand stimuli will decrease in the same order among handedness groups. When there is a mismatch between the hand on the screen and the dominant hand – due to a multisensory integration of the visual input of the spatial configuration ('shape') of the image of a hand on the screen and the proprioceptive input of the response hand (will be explained in more detail in the "wrong hand effect" section below) – the predicted performance order will be reversed among these groups for both left hand and right hand stimuli (see Figure 1b).

Handedness effects on the mental rotation of hands. To my knowledge, only one previous study has tested the influence of handedness on the mental rotation of hands. The researchers used six hand gestures, including one palm-up and five palm-down gestures. They found a reaction time advantage for right hand stimuli in right-handers, but they also showed a speed-accuracy trade-off (Ní Choisdealbha, Brady, & Maguinness, 2011). No difference in performance for left and right hand stimuli was found in left-handers. These results indicate that left-handers and right-handers might have different mechanisms in responding to left hand stimuli and right hand stimuli in the mental rotation of hands. That study used a hand laterality task, which is potentially susceptible to the head motion confounds and verbal labelling errors described earlier. The reaction time peak for the palm-up gesture was at a larger orientation than the five palm-down gestures (270^{o} compared with 180^{o}), indicating that the palm-up gesture is treated differently from other gestures.

This different pattern shown in the palm-up gesture led to further studies on the information processing of hand laterality by contrasting palm-up and palm-down (or back-side of hand) stimuli. These unusual results were important in contrasting two potential theories about the mechanisms of the mental rotation of hands, which will be introduced below.

Sensori-Motor Theories of the Mental Rotation of Hands

Motor simulation theory. The traditional view of the mental rotation of hands is based on the motor simulation theory. Under the motor simulation theory, the motor system that guides the intended action is automatically activated during the mental rotation of hands, which could cause a feeling of moving. This theory suggests an alignment between the spatial representation of the subject's own hand and the image of a hand on the screen: an image of a left hand, for example, will always align with the subject's left hand because the motor system requires a consistent internal representation of body position.

In the 1980s, Lawrence M. Parsons carried out a series of studies to test the motor simulation theory for the mental rotation of hands. In his tasks, participants viewed hand stimuli from different perspectives, with the orientation varying from the normal physical range of motion to an awkward range that is difficult to produce biomechanically (Parsons, 1987). For example, a left hand turned in a counterclockwise direction would be considered an awkward orientation, whereas a left hand turned in a clockwise direction would be considered normal range. Parsons found that across all different views of hand stimuli (back, palm, fingers, wrist, thumb, and little finger viewpoints), response time for awkward orientations was longer than for normal orientations. He also found that, across all hand views, the right and left hand awkward orientations shared reaction time patterns, while the right and left hand normal orientations had reaction time patterns that were similar to each other, but different from the awkward orientations. When the back of the hand was viewed, reaction time increased slightly with each increasing angle of orientation for both normal and awkward orientations. When the palm of the hand was viewed, however, Parsons found a flat reaction time pattern for normal orientations and a pattern with a peak for awkward orientations. Prior to Parsons' work, Sekiyama (1982) studied motor simulation theory by using the same paradigm with five different hand gestures (three in palm-up position, two in palm-down position). Like the Parsons experiments, the reaction time pattern for the degree of clockwise rotations for left hand stimuli was similar to the counterclockwise rotations for right hand stimuli for all gestures. The study also revealed a main effect of hand gesture, such that some gestures had more physically manageable rotations than others. Together, these results indicate that mental rotation of palms is relatively more invariant to changes in orientations than mental rotation of the back of the hand.

It is possible that the handedness of the participants contributed to some of the findings of that study. All participants recruited in Parsons' study (1987) were right-handed. Those right-handed participants were slower overall in responding to left hand stimuli than for right hand stimuli for both the back of the hand and the palm gestures, although this effect was more robust for the back of the hands. This finding suggests right-handers have an advantage in responding to right hand stimuli compared to left hand stimuli, supporting the embodied experience hypothesis.

In order to explore the influence of the hand laterality task itself, Parsons (1987) asked subjects to complete the same experiment by imagining transforming their own hands to the position of the presented hand stimuli. Subjects only needed to verbally report “now” to indicate that they completed the mental spatial transformation. In normal orientations, reaction time was faster for right hands than for left hands when the stimuli were the back of the hands, but this advantage switched to be faster for left hands than for right hands when the stimuli were palms. This result suggests some kind of confusion about the shape of the hand, which will be explicitly discussed in the following section on the “wrong hand effect”. As this study specifically required participants to imagine transforming their own hands, the similar results for both studies suggest that the preferred strategy in this task was to imagine moving one’s hand to simulate the orientation of the stimulus. A similar pattern was also found by contrasting this mental rotation task with physical hand movement (Parsons, 1994), which further supports the motor simulation theory.

The wrong hand effect. Viswanathan et al. (2012) challenged the conventional view of sensorimotor processes underlying the mental rotation of hands (Parsons, Gabrieli, Phelps, & Gazzaniga, 1998; Parsons, 1987, 1994) by proposing a multisensory integration theory (Grafton & Viswanathan, 2014; Viswanathan, Fritz, & Grafton, 2012). Under the multisensory integration theory, information from different sensory modalities integrates to enable a coherent experience of an object. In the case of the mental rotation of hands, the hand stimuli on the screen and the subject’s own hand share a spatial feature (i.e. shape or digit ratio). Because proprioception is the sensory modality that indicates where each body part is, this processing of shared spatial information of hands is explained as a multisensory integration of the visual input of the spatial configuration (‘shape’) of the image of a hand on the screen and the proprioceptive input of the response hand. In the task, the subject's response hands - both left and right hands - are in a palm-down position to make the 'same' and 'different' responses on the keyboard. The shape of a right hand palm-up on the screen will resemble the shape of a left response hand palm-down, creating a shape match. In other words, the shape of a right hand in a *palm-up* gesture on the screen matches the shape of the *palm-down* left hand of the subject making the response, and vice versa for a land hand palm-up.

The researchers found that people's hand laterality judgements can be easily manipulated by the sequence of perceptual processing of the shape and view of a hand (Viswanathan et al., 2012). People processed only shape information when the experimenters presented a visual outline of a hand, without palm or back-of-the-hand details. In this situation, a left palm-up gesture on the screen was recognized as a right hand and vice versa for a right palm-up gesture, suggesting that people processed the shape as the back of the hand. This wrong hand effect could be due to the premature binding of the observer's felt hand, which is palm down, and the palm-up hand on the screen.

However, it is unknown whether shape information is processed separately when both shape and details showing whether it is the palm or back-of-the-hand are presented simultaneously. Furthermore, Viswanathan et al. used the laterality task, so it is unknown whether these results would differ in a same/different task. In order to answer this question, in the present study I tested whether the wrong hand effect exists in the canonical mental rotation of hands by using only stimuli with details clearly showing that it is the palm of the hand.

Hypotheses and Predictions

The goal of present study was to explore the cognitive mechanisms underlying the mental rotation of hands. In this experiment, two groups of subjects (left-handed and right-handed) were recruited to complete a modified SMT with hand stimuli. I started with the goal of purely exploring the influence of world knowledge and embodied experience, but I also needed to address the additional contrasting hypotheses regarding the information processing mechanisms of hand mental rotation (motor imagery and visual-proprioceptive integration). Therefore, I crossed two orthogonal hypothesis axes to yield four competing hypotheses. One axis of the hypothesis space contrasted i) world knowledge of a right-handed world versus ii) embodied experience with one's own hands. The other hypothesis axis contrasted a) motor imagery (i.e. motor simulation/ sensorimotor recalibration) versus b) visual-proprioceptive integration (i.e. multisensory hand binding). A detailed explanation of each of the theories is stated here:

i) World knowledge. Because left-handers and right-handers share the same knowledge of a right-handed world, this theory predicts better performance for right hand stimuli than for left hand stimuli for the mental rotation of hands, for all individuals. A previous study found a consistent advantage for right hand stimuli, but they only recruited right-handed subjects (Parsons, 1987). If all subjects respond faster or more accurately to right hand stimuli, then this hypothesis would be supported.

ii) Embodied experience. An alternative theory is that people respond better for hand stimulus that matches their dominant hand. If left-handers respond faster or more accurately for left hand stimuli and right-handers respond faster or more accurately for right hand stimuli, then the embodied experience hypothesis would be supported.

a) Motor imagery. Motor imagery (i.e., motor simulation theory) refers to the idea that the motor system that guides the intended action is automatically activated during the mental rotation of hands. It represents the match of the holistic representation of subject's own hands (i.e. shape, view, details, etc.) and the hand seen on screen, because the motor system requires a consistent internal representation of body position. Purely under this hypothesis without considering the influence of embodied experience or world knowledge, a match between a subject's dominant hand and the hand stimuli on the screen would have no effect on performance. Note that the prediction of this theory is invariant to the perspective of the hand stimuli (e.g. back- or palm- side) on its own. While this hypothesis cannot be demonstrated on its own, i.e., it cannot indicate how handedness influences performance, it serves to account for the mechanism in combination with world knowledge or embodied experience. For example, if right-handers responded better for right hand stimuli than for left hand stimuli, then motor imagery and world knowledge theories are supported. If right-handers responded better for left hand stimuli than for right hand stimuli, then the motor imagery theory is not correct (see Figure 1a).

b) Visual-proprioceptive integration. Under this theory, a 'wrong hand effect' will be expected, whereby the match of spatial configuration ('shape') of the hand stimuli on the screen and the proprioceptive information from the hand making the response is preferentially processed. The shape of a right palm-up hand on the screen resembles a left palm-down hand. I tested palm-up stimuli for this task, and the hand making the response in this task was in a palm-down position on the keyboard. Thus, this theory predicts that right-handed subjects will perform better for left hand stimuli than for right hand stimuli and vice versa for left-handed subjects, which is contrary to the prediction of motor imagery theory.

These two sets of theories represent orthogonal features in the mental rotation of hands. In order to fully test the interaction of these two sets of theories, I crossed these two pairs of theories to yield four specific hypotheses (see Figure 1a). To distinguish between these four hypotheses, I tested both left-handed and right-handed subjects and incorporated left and right hand stimuli on the screen.

Hypothesis 1: Motor Imagery and World Knowledge

Prediction: First, based on motor imagery theory, a left palm-up hand stimulus will be recognized as a left hand, and a right palm-up hand stimulus will be recognized as a right hand. Second, based on world knowledge theory, everyone will be more familiar with right hands than with left hands. Therefore, all subjects' performance for right hand stimuli will be better than for left hand stimuli.

Hypothesis 2: Motor Imagery and Embodied Experience

Prediction: First, based on motor imagery theory, a left palm-up hand stimulus will be recognized as a left hand, and vice versa for right hands. Second, based on embodied experience theory, people will perform better on stimuli that match their dominant hands than on stimuli that match their non-dominant hands. Therefore, left-handers will perform better for left hand stimuli and right-handers will perform better for right hand stimuli.

Hypothesis 3: Visual-proprioceptive Integration and World Knowledge

Prediction: First, based on visual-proprioceptive integration theory, a left palm-up hand stimulus will be recognized as a right hand, and vice versa for right hands. Second, based on world knowledge theory, everyone will be more familiar with right hands than with left hands. Therefore, under this hypothesis, all subjects' performance for left hand stimuli will be better than for right hand stimuli.

Hypothesis 4: Visual-proprioceptive Integration and Embodied Experience

Prediction: First, based on visual-proprioceptive integration theory, a left palm-up hand stimulus will be recognized as a right hand, and vice versa for right hands. Second, based on embodied experience theory, people will perform better on stimuli that match their dominant hands than on stimuli that match their non-dominant hands. Therefore, for left-handers, performance for right hand stimuli will be better than for left hand stimuli. For right-handers, performance for left hand stimuli will be better than for right hand stimuli.

Other Possible Factors

Besides handedness direction, some other factors might influence subjects' performance. Although I tried to control the influence of these factors in our experimental design, it is still possible that they could influence the outcomes. Thus, I will still consider them at a later point in our data analysis in order to have a more thorough understanding of the results. Here I introduce some of the main possible factors and how I tried to control them.

Hand gestures. Most previous studies on the mental rotation of hands only used one gesture as stimuli, usually an open palm gesture. This use of a single gesture could be one factor leading to the ceiling effect of accuracy in previous studies (e.g. de Lange, Helmich, & Toni, 2006; Lawrence M. Parsons, 1987; Zapparoli et al., 2014). In order to preclude the ceiling effect, one more gesture (a pointer - a hand in a pointing gesture) was included in the current study to increase the difficulty of the test. The task was to judge whether the two hands shown were the same hand. To make the task even more challenging, I also included a condition in which the two hand stimuli were different gestures (one pointer, one palm). Because of these modifications, I expected that response accuracy could become another performance indicator in the study, in addition to reaction time. Although I counterbalanced the order and amount of different gestures, it is still possible that subjects' performance varied among different gestures.

Response pattern. Here, response pattern refers to which hand pressed the "same" response and which hand pressed the "different" response. For this study, there were two response patterns: left hand pressed "same", right hand pressed "different"; or left hand pressed "different", right hand pressed "same". I counterbalanced this factor by randomly assigning half of the subjects in each handedness group to complete the task in each response pattern. I labeled an "S" button to represent "same" and a "K" button to represent "different". When subjects were assigned to use their left hand to press "same" and right hand to press "different", the "S" button was put on the left while the "K" button was put on the right; the position of two buttons were switched when subjects were assigned to the other response pattern. However, I noticed later that the position of the "S" key on a standard keyboard is always on the left, so subjects might find it easier to press "S" with their left hand.

Strategy. Two strategies could be used in this hand mental rotation task: mental rotation and thumb strategies. Mental rotation means solving the problem purely by mentally rotating one hand stimulus to match the other one. The thumb strategy is a trick, comparing whether the thumb is on the same side of each hand stimuli. For example, if there are two left hands on the screen, both thumbs are on the left side of each hand because all hand stimuli in this experiment were palm-up. If one hand is a left hand and the other hand is a right hand, then one thumb will be on the left, one thumb will be on the right. As mentioned above, extreme handers tend to be less flexible than mixed handers. Thus, it is possible that mixed handers would have a higher frequency applying the thumb strategy, while extreme handers tend to rely on mental rotation. Therefore, I asked subjects to verbally report their strategies after they finished the experiment to look at the potential differences in strategies among handedness groups.

Methods

Participants

Participants consisted of 69 (41 females) University of California, Santa Barbara undergraduates who participated in return for course credit. Participants were discarded from data analysis for using their own hands to simulate hand stimuli (*n* =2) or having a high proportion of reaction time outliers (*n* =1). The direction and strength of each person's handedness was tested by the Edinburgh Handedness Inventory (see Appendix) (Oldfield, 1971). The final analysis included 33 left-handers and 33 right-handers: 23 mixed left-handers (14 females), 10 extreme left-handers (7 females), 16 mixed right-handers (8 females), and 17 extreme right-handers (10 females). Ages of the remaining 66 participants ranged from 18 to 24 (mean 19.70; 2 participants did not report their ages). All participants signed an informed consent form in agreement with the UCSB Institutional Review Board requirements in accordance with the Declaration of Helsinki.

Stimuli

I used a modified Shepard and Metzler task (SMT) with hand stimuli, which were adapted from a previous study (Sperry, 1968). All stimuli were palm-side up but could either have the palm open or be closed in a pointing gesture (see Figure 2). All images (500 × 500 pixels for each image) were displayed to the participants on a 15-inch computer monitor (display resolution at 1920×1080 pixels) using E-prime 2.0 software (Schneider, Eschman, & Zuccolotto, 2012). One hand was displayed on the left side of the screen and one hand was displayed on the right side of the screen for each trial.

Design

A 2 (handedness direction: left-handed, right-handed; between subjects) × 2 (handedness strength: left-handed, right-handed; between subjects) × 2 (stimuli condition: the two stimuli showed the same hand, or they showed different hands; within subjects) × 2 (gesture type: same gesture, different gesture; within subjects) × 2 (subtypes of each gesture type: palm-palm and pointer-pointer for the same gesture combination, palm-pointer (palm on the left) and pointer-palm (palm on the right) for the different gesture combination; within subjects) × 10 (the angular disparity between the two hands: 10 different magnitudes ranges from 0^o to 180^o in 20^o steps, but not all subtypes of gesture combinations included all of the possible angular disparities; within subjects). The position of the hands was counterbalanced such that a left hand could appear equally as often on the left side of the screen as on the right side. Therefore, there were 160 trials in total (2 handedness combinations of hand stimuli tested × 2 same/different hand × 2 same/different gesture × 2 counterbalancing positions × 10 angular disparities) (Figure 2). These 160 trials were randomly separated into 2 blocks with a short break in between. All stimuli were presented in random order for all participants.

Procedure

Subjects first were greeted in the lab, given information about the study, and given consent forms to sign. They then completed the Edinburgh Handedness Inventory (EHI; see Appendix). The EHI questionnaire contains 10 items of daily behaviors (e.g. writing). Subjects were asked to fill in blanks with "+" or "+ +" indicating the frequency of using their left hand or right hand for those behaviors in daily life, with "+ +" indicating greater frequency.

Next, they were given instructions and performed the mental rotation of hands task. Subjects sat approximately 50 cm in front of the computer screen. They were first presented with instructions to understand the task, then started with four practice trials (stimuli were different from experimental trials) before beginning the formal experiment. Each trial started with a fixation cross for 1000 milliseconds as the inter-trial interval. Then two hand stimuli were presented simultaneously on the left and right of the screen. Subjects were asked to judge whether the two hand stimuli were the same hands or were different hands (Figure 3). They used one hand to press a key to indicate that the stimuli were the same hands and used the other hand to press another key to indicate that the stimuli were different hands; whether the hand used to respond to the 'same' trials was their dominant hand or nondominant hand was counterbalanced across subjects. Subjects were instructed to respond as quickly and accurately as possible. The 1000ms fixation cross for the next trial started automatically as soon as subjects pressed a response key. Accuracy and reaction time for each trial were recorded. Finally, participants were asked to verbally report their strategy in completing the tasks, which the experimenter wrote down.

Data Analysis

We evaluated subjects' handedness direction and strength based on their EHI score. The laterality quotient (LQ) was calculated based on the sum of the left "+" marks (L) and the sum of the right "+" marks (R):

$$LQ = (R - L)/(R + L) \times 100$$

We measured each subject's handedness direction and handedness strength based on the criteria used in previous studies (Christman & Butler, 2011; Hardie & Wright, 2014; Lyle & Orsborn, 2011; Smit, Kooistra, van der Ham, & Dijkerman, 2017; Westfall, Jasper, & Christman, 2012). For handedness *direction*, if the LQ score was within the range of -1 to -100, then the subject was considered left-handed. If the LQ score was within the range of +1 to +100, then subject was considered right-handed. For handedness *strength*, if the LQ score was between -80 to +80, then the handedness strength was mixed. If the LQ score fell in ranges of either -100 to -80 or +80 to +100, then the handedness strength was assigned as extreme (see Figure 4).

For the task data, I first removed outliers that were below or above 2 standard deviations of the mean of each subject's reaction time; approximately 1.78% of trials were removed. Then I calculated the accuracy of the remaining trials. The reaction times for each condition were calculated only based on correct trials. Because mental rotation of stimuli in 'different' trials to achieve congruency cannot be defined, previous studies usually only analyzed 'same' trials (e.g. Shepard & Metzler, 1971). To examine the effect of the laterality of the hand stimuli (left hands vs right hands), I had to use pairs which displayed either both left or both right hands; mismatches display both hands and therefore are ambiguous. Therefore, for the subsequent analysis, I only examined trials on which the two hands on the screen were the same, either both right hands or both left hands. Prior to the formal data analyses, I conducted overall analyses of the full dataset to gain knowledge of the homogeneity of the dataset under each condition. For the data analysis, I conducted a 2 (handedness direction: left handed, right handed) × 2 (hand stimuli tested: left hands, right hands) × 2 (handedness strength: extreme, mixed) mixed ANOVA only on same hand trials. “Hand stimuli tested” was a within-subject factor while “handedness direction” and “handedness strength” were between-subject factors. In data analysis, I did not consider gesture combination as a factor in our analysis because the inclusion of different gestures was mainly designed to increase task difficulty and was not a primary factor of interest. I did not consider response pattern (which hand was used to press “same” or “different” key) because the counterbalanced design minimized the influence of the response hand. I also did not have sufficient power to conduct analysis on the angular disparity. R-studio was used for all data analysis.

Results

Overall Analyses

I first wished to examine the overall effects of both between-subject and within-subject factors. This is a general assessment of the data distribution in all related factors rather than in-depth data analyses to answer the research questions, which will be explicitly discussed in the next section. For the between-subjects effects, I conducted two-sample t-tests on the accuracy and reaction time of all trials (both “same” and “different” trials) on the primary variables of handedness direction, handedness strength, and response pattern (whether the left hand pressed “same” and the right hand pressed “different” or vice versa). Because sex differences have been previously found in mental rotation studies (e.g., Voyer, Voyer, & Bryden, 1995), I also conducted a two-sample t-test on sex. Left-handers (M = 88% ± 1%, 3382 ± 184 ms) and right-handers (M = 89% ± 2%, 3126 ± 222 ms) had no difference in accuracy ($t(64) = -0.53$, $p = 0.6$, $d = -0.13$, *ns*) or reaction time ($t(64) = 0.89$, $p = 0.38$, $d = 0.218$, *ns*). There was no difference between extreme-handed individuals (M = 90% ± 1%, 3281 ± 204 ms) and mixed-handed individuals (M = 88% ± 2%, 3235 ± 201 ms) in accuracy ($t(64) = -0.89$, $p = 0.38$, $d = -0.223$, *ns*) or reaction time ($t(64) = -0.16$, $p = 0.88$, $d = -0.039$, *ns*). In terms of response pattern, there was no difference between the left hand pressing “same” - right hand pressing “different” (M = 88% ± 2%, 3108 ± 183 ms) and the right hand pressing “same” – left hand pressing “different” (M = 89% ± 2%, 3409 ± 225 ms) in either accuracy ($t(64) = -0.53$, $p = 0.6$, $d = -0.131$, *ns*) or reaction time ($t(64) = -1.04$, $p = 0.3$, $d = -0.257$, *ns*). There was no difference between males (M = 90% ± 2% *s.e.*, 3331 ± 262 *s.e.* ms) and females (M = 88% ± 1%, 3201 ± 166 ms) in either accuracy ($t(64) = 0.59$, $p = 0.56$, *Cohen’s d* = 0.147, *ns*) or reaction time ($t(64) = 0.44$, $p = 0.66$, $d = 0.111$, *ns*).

For the within-subjects effects, I conducted paired t-tests on the accuracy and reaction time of all trials on same versus different hand stimuli and same versus different hand stimuli gesture. I found no difference in accuracy between same hand trials (M = 89% ± 1%) and different hand trials (M = 89% ± 1%) ($t(65) = -0.43$, $p = 0.67$, $d = -0.053$, *ns*), but the reaction time for same hand trials (M = 3058 ± 137 ms) was significantly faster than for different hand trials (M = 3463 ± 159 ms) ($t(65) = -6.28$, $p < 0.001$, $d = -0.773$). As for the gesture of the hand stimuli, there was no difference in accuracy ($t(65) = -0.24$, $p = 0.812$, $d = -0.029$, *ns*) between same stimuli gestures (M = 89% ± 1%) and different stimuli gestures (M

= 89% ± 1%), but reaction time was significantly shorter ($t(65) = -5.16$, $p < 0.001$, $d = -0.635$) for same stimuli gestures ($M = 3087 \pm 138$ ms) than for different stimuli gestures ($M = 3440 \pm 156$ ms).

Analysis of Handedness Direction, Handedness Strength, and Hand Stimuli Tested

Same hand trials. I first conducted a 2 (handedness direction: left handed, right handed) × 2 (hand stimuli tested: left hands, right hands) × 2 (handedness strength: extreme, mixed) ANOVA on trials in which both stimuli were of the same hand. For accuracy, I found no main effects of handedness direction ($F(1,62) = 1.62$, $p = 0.21$, $\eta_p^2 = 0.03$, *ns*), hand stimuli tested ($F(1,62) = 0.06$, $p = 0.8$, $\eta_p^2 = 0.001$, *ns*), or handedness strength ($F(1,62) = 0.17$, $p = 0.68$, $\eta_p^2 = 0.003$, *ns*). I found no two-way interaction either between handedness direction and hand stimuli tested ($F(1,62) = 0.49$, $p = 0.49$, $\eta_p^2 = 0.008$, *ns*) or between handedness strength and hand stimuli tested ($F(1,62) = 0.03$, $p = 0.86$, $\eta_p^2 = 0.0005$, *ns*). I found a marginally significant interaction between handedness direction and handedness strength ($F(1,62) = 3.28$, $p = 0.07$, $\eta_p^2 = 0.05$). I found no three-way interaction among handedness, hand-tested, and strength in accuracy ($F(1,62) = 2.59$, $p = 0.11$, $\eta_p^2 = 0.04$, *ns*).

For reaction time, I found no main effect of handedness direction ($F(1,62) = 0.15$, $p = 0.7$, $\eta_p^2 = 0.002$, *ns*) or handedness strength ($F(1,62) = 0.01$, $p = 0.93$, $\eta_p^2 = 0.0001$, *ns*). I found a marginal main effect of hand stimuli tested ($F(1,62) = 3.33$, $p = 0.07$, $\eta_p^2 = 0.05$) that the reaction time for right hand stimuli ($M = 3024 \pm 100$ ms) was somewhat faster than for left hand stimuli ($M = 3150 \pm 118$ ms). I found no two-way interaction between handedness direction and hand stimuli tested ($F(1,62) = 1.46$, $p = 0.23$, $\eta_p^2 = 0.02$, *ns*), between handedness strength and hand stimuli tested ($F(1,62) = 0.94$, $p = 0.33$, $\eta_p^2 = 0.02$, *ns*), or between handedness direction and handedness strength ($F(1,62) < 0.01$, $p = 0.97$, η_p^2

< 0.0001, *ns*). I found a marginally significant three-way interaction among handedness, hand-tested, and strength in reaction time ($F(1,62) = 2.98$, $p = 0.09$, $\eta_p^2 = 0.05$, *ns*).

Same gesture and different gestures. As half of the same hand trials were different gestures (one pointer, one palm), which has not been tested in previous studies, there might be a difference in performance between same gesture (both palms or both pointers) and different gestures (one palm and one pointer). Therefore, I conducted a 2 (hand stimulus: same, different) × 2 (gesture: same, different) repeated-measures ANOVA on all trials (including both 'same' and 'different' hand stimuli trials). For accuracy, I found similar results as in the overall analysis, such that there were no main effect of same/different gesture or same/different hand stimulus. This time, I found no interaction between the two ($F(1,65) = 0.03$, $p = 0.87$, $\eta_p^2 = 0.0004$, *ns*). Results similar to the overall analysis were also found for reaction time: there was a main effect of gesture ($F(1,65) = 24.13$, $p < 0.001$, $\eta_p^2 = 0.27$) with same gesture hand stimuli ($M = 3087 \pm 138$ ms) faster than for different gesture hand stimuli ($M = 3440 \pm 156$ ms). There was also a main effect of same/different hand stimulus ($F(1,65) = 30.38$, $p < 0.001$, $\eta_p^2 = 0.32$) with same hand stimuli ($M = 3057 \pm 137$ ms) faster than different hand stimuli ($M = 3463 \pm 159$ ms). There was no interaction ($F(1,65) = 2.94$, $p = 0.09$, $\eta_p^2 = 0.04$, *ns*) between the two. These results indicate that even within same hand stimuli, responding to different gestures was more difficult than when the gestures were the same. On the one hand, it means that I did make the test harder by using different gestures. On the other hand, this difference could overshadow potential three-way interactions, such that the different gesture trials may have affected the aggregated results. Therefore, it is necessary to apply this analysis on each gesture independently.

Same hand/same gesture. I conducted a 2 (handedness direction: left handed, right handed) × 2 (hand stimuli tested: left hands, right hands) × 2 (handedness strength: extreme, mixed) ANOVA on trials where the hand stimuli on the screen were both left hands or both right hands, and they were both making the same gesture ("same hand/same gesture"). For accuracy, I found no main effect of handedness direction ($F(1,62) = 2.29$, $p = 0.14$, $\eta_p^2 = 0.04$, *ns*), hand stimuli tested ($F(1,62) = 0.57$, $p = 0.45$, $\eta_p^2 = 0.009$, *ns*), or handedness strength ($F(1,62) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.003$, *ns*). I found no two way interaction either between handedness direction and hand stimuli tested ($F(1,62) = 1.49$, $p = 0.23$, $\eta_p^2 = 0.02$, *ns*) or between handedness strength and hand stimuli tested ($F(1,62) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.003$, *ns*). I found a significant interaction between handedness direction and handedness strength ($F(1,62) = 4.99$, $p = 0.03$, $\eta_p^2 = 0.07$). Tukey post-hoc tests revealed that extreme right-handers ($M = 92\% \pm 1\%$) had marginally higher accuracy than extreme left-handers ($M = 83\% \pm 3\%$, $p = 0.084$) for same hand/same gesture trials. Finally, I found a significant three-way interaction among handedness direction, hand stimuli tested, and handedness strength ($F(1, 62) = 6.43$, $p =0.01$, $\eta_p^2 = 0.09$).

Tukey post-hoc tests for the three-way interaction revealed that mixed right-handers had higher accuracy for left hand stimuli ($M = 92\% \pm 2\%$) than for right hand stimuli ($M = 83\% \pm 6\%$, $p = 0.014$). This result indicates that mixed right-handers had an advantage for non-dominant hand stimuli than for dominant hand stimuli, which supports Hypothesis 3 and Hypothesis 4. Further analysis between handedness groups' performance found that extreme right-hander's accuracy for right hand stimuli ($M = 93\% \pm 1\%$) was slightly higher than both mixed right-hander's ($M = 83\% \pm 6\%$, $p = 0.07$) and extreme left-hander's accuracy for right hand stimuli ($M = 81\% \pm 4\%$, $p = 0.075$); both results support Hypothesis 2. These finegrained results of handedness strength could explain the previous null results, since the extreme hander's and mixed hander's were averaged over hand stimuli tested.

For reaction time, I found no main effect of handedness direction ($F(1,62) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.003$, *ns*), hand stimuli tested ($F(1,62) = 1.11$, $p = 0.3$, $\eta_p^2 = 0.02$, *ns*), or handedness strength ($F(1,62) = 0.03$, $p = 0.86$, $\eta_p^2 = 0.0005$, *ns*). I found no two-way interaction either between handedness direction and handedness strength ($F(1,62) = 0.07$, $p = 0.8$, $\eta_p^2 = 0.001$, *ns*), between handedness strength and hand stimuli tested ($F(1,62) = 0.28$, $p = 0.6$, $\eta_p^2 = 0.005$, *ns*), or between handedness direction and hand stimuli tested ($F(1,62) = 0.01$, $p = 0.94$, $\eta_p^2 < 0.0001$). However, I found a three-way interaction among handedness direction, hand stimuli tested, and handedness strength in reaction time ($F(1,62) = 8.34$, $p = 0.005$, $\eta_p^2 = 0.12$). Tukey post-hoc tests revealed that mixed right-handers responded faster for right hand stimuli ($M = 2514 \pm 289$ ms) than for left hand stimuli ($M = 3012 \pm 484$ ms, $p = 0.023$). Here, the advantage of mixed right-handers for right hand stimuli supports Hypothesis 1 and Hypothesis 2.

Same hand/same gesture: mixed-handed group. Mixed right-handers' higher accuracy for left hand stimuli and shorter reaction time for right hand stimuli caused a trade-off effect. This actually replicates the results of a previous study (Ní Choisdealbha et al., 2011), although that study used a hand laterality task instead of the same/different task. Thus, the overall results from the same hand stimuli/same gesture trials do not strongly support any of the hypotheses. Considering that extreme right-handers had an overall better performance than extreme left-handers and that extreme left-handers had a smaller sample size than the other three handedness groups, the data pattern in the mixed-handed group may be overshadowed in the three-way ANOVA analysis that included extreme-handed groups.

Therefore, I extracted data just for the mixed-handed groups for a *handedness direction* × *hand stimuli tested* two-way ANOVA analysis.

For accuracy, there was no main effect on handedness direction (F(1,37) = 0.26, p = 0.61, η_p^2 = 0.007, *ns*) or hand stimuli tested (F(1,37) = 0.61, p = 0.44, η_p^2 = 0.02, *ns*), but there was a significant interaction between the two factors (F(1,37) = 6.44, p = 0.02, η_p^2 = 0.15). Although Tukey post-hoc tests did not find significant differences, the data pattern still shows a "wrong hand effects" tendency: mixed left-handers tended to have higher accuracy for right hand stimuli (M = 91% ± 2%) than for left hand stimuli (M = 86% ± 2%); mixed right-handers tended to have higher accuracy for left hand stimuli (M = 92% ± 2%) than for right hand stimuli (M = 83% ± 6%); mixed left-handers (M = 91% ± 2%) tended to have higher accuracy than mixed right-handers for right hand stimuli (M = 83% ± 6%). These results all showed a tendency that mixed handed groups had an advantage for non-dominant hand stimuli than for dominant hand stimuli, which supports Hypothesis 4.

For reaction time, there was no main effect on handedness direction (F(1,37) = 0.22, p = 0.64, η_p^2 = 0.006, *ns*) or hand stimuli tested (F(1,37) = 1.41, p = 0.24, η_p^2 = 0.04, *ns*). There was a significant interaction between the two factors (F(1,37) = 4.94, p = 0.03, η_p^2 = 0.12), but post-hoc tests did not find any significant differences.

Same hand/same gesture: extreme-handed group. Correspondingly, I extracted data for the extreme-handed groups for a *handedness direction* × *hand stimuli tested* two-way ANOVA analysis.

For accuracy, I found a main effect of handedness direction (F(1,25) = 8.85, p = 0.006, η_p^2 = 0.26) that extreme right-handers (M = 92% ± 1%) had overall higher accuracy than extreme left-handers (M = 83% ± 3%). There was no main effect of hand stimuli tested

($F(1,25) = 0.12$, $p = 0.73$, $\eta_p^2 = 0.005$, *ns*) or any interaction between the two factors ($F(1,25) = 1.59$, $p = 0.22$, $\eta_p^2 = 0.06$, *ns*).

For reaction time, there was no main effect of handedness direction ($F(1,25) = 0.01$, $p = 0.92$, $\eta_p^2 = 0.0004$, *ns*) or hand stimuli tested ($F(1,25) = 0.14$, $p = 0.71$, $\eta_p^2 = 0.005$, *ns*), but there was a marginally significant interaction between the two factors ($F(1,25) = 3.94$, $p = 0.06$, $\eta_p^2 = 0.14$).

Palm-palm versus pointer-pointer gesture types. I also decided to look at the influence of gesture types within same gesture trials. I broke the trials down to two gesture types (palm-palm, pointer-pointer) and analyzed their data in a 3-way analysis (handedness direction, handedness strength, and hand stimuli tested) to see if the same patterns occurred for both palm-palm trails and pointer-pointer trials. The same pattern was found for both gesture types.

Strategy Use

There were two main strategies reported in the hand mental rotations task: the mental rotation strategy and the thumb strategy (Figure 6a). When a person uses the mental rotation strategy, they mentally rotate one hand to align with the other hand in order to judge whether the two hands are the same. The thumb strategy compares the relative position of the thumb in each hand. If the thumb was on the right in both hand stimuli, for example, then the two hand stimuli were the same hand. If the thumb was on the right of one hand, but on the left of the other hand, the two hand stimuli were different hands. Both mental rotation and thumb strategies were reported in all of the four handedness groups (extreme and mixed left- and right-handers; Figure 6b). Each individual reported only one strategy except one extreme right-hander who reported using both strategies.

Chi square tests of independence revealed no significant difference among the four handedness groups on the two strategies (leaving out the subject who applied both strategies) ($\chi^2(3, N = 65) = 2.026$, $p = 0.567$, *ns*). I also performed separate chi square tests on the relationship between strategy use and handedness direction ($\chi^2(1, N = 65) = 0.016$, $p = 0.9$, *ns*) and handedness strength ($\chi^2(1, N = 65) = 1.357$, $p = 0.244$, *ns*), but no relationship was found. Further, I performed a 2 (handedness direction) × 2 (handedness strength) × 2 (strategy: mental rotation, thumb strategy) log linear analysis on subjects' frequency of reported strategy use, but there were no main effects or interactions between handedness direction, handedness strength, and strategy (all $p > 0.1$). Although there was a higher proportion of subjects using the thumb strategy in the mixed-handed groups (56%) than in the extreme-handed groups (38%, not including the individual who applied both strategies), the difference was not statistically significant.

I further wanted to examine subjects' strategies when the stimuli showed two different gestures. With two gestures, subjects could choose to mentally open the pointer to match the palm or close the palm to match the pointer. To test this question, I ran an additional 20 -30 trials from the same experiment on five subjects after they finished the formal experiment. While completing these additional exploratory trials, subjects were asked to orally report their answer and were allowed to use their own hands to simulate as much as they want. The experimenter pressed the response key for the subjects in each trial to make the test move on. Surprisingly, none of the subjects used their own hands to simulate the hand stimuli even though they were allowed to. It is possible that these subjects adapted to the test mode of not using their own hands from the formal experiment. Then I asked these subjects after they had finished the additional trials whether they tended to mentally open pointers or close palms in completing trials with different gestures. All five subjects reported that they only mentally opened pointers, except one subject who reported using both strategies.

Discussion

The goal of current study was to understand the mechanisms underlying the mental rotation of hands. I tested these mechanisms by applying a modified Shepard & Metzler test with hand stimuli on left- and right-handed people. In same hand/same gesture trials, I found a speed-accuracy trade-off for mixed right-handers: they had higher accuracy for left hand stimuli than for right hand stimuli, but shorter response times for right hand stimuli than for left hand stimuli. Comparing across the handedness groups, extreme right-handers had higher accuracy than mixed right-handers for right hand stimuli.

Comparison of Hypotheses

Each of the four hypotheses will be discussed along with the results below. The results mentioned below came from analysis at same hand/same gesture level if not specified.

Hypothesis 1 corresponds to the combination of the motor imagery and world knowledge theories. This hypothesis predicts that all subjects' responses would be better for right hand stimuli than for left hand stimuli, and there would be no handedness group difference either for left hand stimuli or for right hand stimuli. This prediction was supported by the result that mixed right-handers responded faster for right hand stimuli than for left hand stimuli. However, this support is compromised due to a speed-accuracy trade-off, such that mixed right-handers had higher accuracy for left hand stimuli than for right hand stimuli. Mixed left-handers having higher accuracy tendency for right hand stimuli than for left hand stimuli provides some support for Hypothesis 1, but this result was also predicted by Hypothesis 4. Further support comes from no between-group difference for left hand stimuli, but this result was predicted by both Hypothesis 1 and Hypothesis 3, and is a null prediction, so it does not provide strong support.

Hypothesis 2 is the combination of the motor imagery and embodied experience theories. This hypothesis predicts that left-handers would respond better for left hand stimuli than for right hand stimuli and right-handers would respond better for right hand stimuli than for left hand stimuli. It also predicts that people with stronger right hand strength would have better performance than people with weaker right hand strength for right hand stimuli, and vice versa for left hand strength. This prediction was supported by the result that extreme right-handers had marginally higher accuracy than mixed right-handers and extreme left-handers for right hand stimuli. However, this support is not very strong because both results are marginally significant.

Hypothesis 3 is a combination of visual-proprioceptive integration and world knowledge theories. This hypothesis predicts that both left-handers and right-handers would respond better for left hand stimuli than for right hand stimuli, and there would be no handedness group difference either for left hand stimuli or for right hand stimuli. As mentioned before, I found that mixed right-handers had higher accuracy for left hand stimuli than for right hand stimuli, but this result was compromised by the speed-accuracy trade-off effect. Additionally, I found no between-group difference for left hand stimuli, which provides weak support for this hypothesis.

Hypothesis 4 is a combination of visual-proprioceptive integration and embodied experience theories. This hypothesis predicts that left-handers would respond better for right hand stimuli than for left hand stimuli and that right-handers would respond better for left hand stimuli than for right hand stimuli. It also predicts that people with stronger right hand strength would have worse performance for right hand stimuli than people with weaker right hand strength, and vice versa for left hand strength. The support for this hypothesis first came from the result that mixed right-handers had higher accuracy for left hand stimuli than for right hand stimuli, which is weak due to the speed-accuracy effect. The second support for this result is that mixed left-handers had higher accuracy tendency for right hand stimuli than for left hand stimuli. The third support for this result is that mixed left-handers had higher accuracy tendency than mixed right-handers for right hand stimuli.

Within Extreme- and Mixed-Handed Groups

As mixed-handed groups and extreme-handed groups showed quite different patterns of results, I start with discussing results within each strength group separately.

Mixed-handed groups: embodied experience and visuo-proprioceptive integration. Mixed left-handers' better performance trend for their nondominant hand and their better performance trend than mixed right-handers for right hand stimuli converge on Hypothesis 4, embodied experience and visuo-proprioceptive integration theories. Mixed right-handers' seemingly conflicting within-group accuracy and reaction time results could have two possible interpretations. The first interpretation is to consider the conflicting results as a speed-accuracy trade off, which does not really support any hypothesis but also does not go against Hypothesis 4. An alternative speculation is that accuracy and reaction time represent discrete processes in the mental rotation task: accuracy reflects the thinking process because the judgement is produced during the thinking process, while reaction time reflects the execution process (i.e., physical response to carry out the judgement). Following this interpretation and assuming hand making the response does not play a role because the variable of response pattern is already controlled in the experimental design, accuracy would be the primary indicator, because all of the theories explain the underlying mechanism during the thinking process of mental rotation. In that case, mixed right-handers' higher accuracy for their non-dominant hand stimuli than for their dominant hand stimuli adds more support to Hypothesis 4. Overall, Hypothesis 4 is most strongly supported in mixed-handed groups.

Extreme-handed groups. Extreme-handed groups showed a very different pattern of results than mixed-handed people. Extreme right-handers had overall higher accuracy than extreme left-handers averaged over both left hand stimuli and right hand stimuli. Although the analysis revealed that extreme right-handers had better performance for right hand stimuli than extreme left-handers, in support of Hypothesis 2, it could be due to the overall performance discrepancy between the two extreme-handed groups. Additionally, extreme left-handers had a small sample size (10 subjects) which decreased the power of the data analysis and the cogency of potential data interpretations regarding this group. Thus, no particular Hypothesis can suitably explain the performance within extreme-handed groups in this study.

Between Extreme- and Mixed-Handed Groups

Left hand stimuli: world knowledge. There was no performance discrepancy among all the four handedness groups for left hand stimuli. This result only fits the null prediction of Hypothesis 1 and Hypothesis 3. More specifically, it indicates no embodiment effects, in spite of motor imagery or visual-proprioceptive integration. World knowledge might instead be involved during the response to left hand stimuli for all people, although this support is weak.

Right hand stimuli: world knowledge and embodied experience. Despite homogenous performance for left hand stimuli, there were inconsistent results for right hand stimuli between the extreme-handed group and the mixed-handed group. If there only exists the influence of embodied experience during the response to right hand stimuli, regardless of motor imagery or visual proprioceptive integration, then performance should either increase or decrease in a set order: extreme left-handers, mixed left-handers, mixed right-handers, extreme right-handers. If there is additional influence of world knowledge for right hand stimuli, this factor is assumed to influence each handedness group similarly. Therefore, the predicted performance rank should stay the same, since adding the same weight does not change relative weight on the scale. However, the "disrupted" order of the results for right hand stimuli (rank in decrease: extreme right-handers, mixed left-handers, mixed right-handers, extreme left-handers) suggests an additional influence of world knowledge that varies among the handedness groups.

The speculation that world knowledge impacts each handedness group differently has some empirical evidence from animal studies. In 1975, scientists created a left-handed world for right-handed mice and a right-handed world for left-handed mice (Collins, 1975). Their results support the hypothesis that handedness can adapt to the predominant cues in the world. In the left-handed world, some right-handed mice adapted to the world and became left-handers, while the remaining right-handed mice continued to use their right hand. An analogous adaptation occurred to those left-handed mice in the right-handed world: some left-handers turned into right-handers, while the remaining left-handed mice continued to use their left hand for food. This adaptation provides a model for mixed handed groups in human studies, especially in explaining the conflicting results between the mixed-handed group and the extreme-handed group in the current study. Assuming there were equal numbers of left-handers and right-handers in the beginning, some left-handers adapted to the right-handed world and become mixed right-handers, which leads to an imbalanced ratio of left-handers and right-handers in the world. In that case, the mixed right-handers were likely more strongly affected by right-handed world knowledge than the extreme right-handers since world knowledge modified their embodied experience.

Follow-up Studies

Although the current study ended with somewhat mixed results, some possible follow-up studies might give a clearer answer to the question. One solution is to only test extreme-handers since they might be less susceptible to adapting to world knowledge. I could prescreen volunteering participants until I get the extreme-handers I need. Another solution is to only use right hand stimuli in a modified paradigm, because no between-group differences were found for left hand stimuli. More trials for right hand stimuli could bring more power to the results. I could also include only palm stimuli instead of pointers or mixed gestures. Because mixed gestures made the test more difficult, it might have overshadowed any potential handedness effects. Thus, I ended up mainly focusing on trials with same gestures. I could also change the response pattern from using hands to using non-manual responses such as verbal report, since a few subjects reported that pressing “S” with their right hand went against their typical experience. To fully test the wrong hand effect, I can also include the back side of hands as stimuli, rather than just palms. In addition, if I used fewer experimental conditions, I could include a wider spectrum of angular disparities so that I could thoroughly consider the orientation of the stimulus. Finally, although I did not find sex differences in this study, the power to detect potential effects was limited by the sample size.

The current study supports a mixed influence of embodied experience over world knowledge only at the figural scale, which is “small in scale relative to the body and external to the individual, and can be apprehended from a single viewpoint” (Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006). Because of the small scale, the results could be specific to this task. Thus, it is unknown whether world knowledge and embodied experience will contribute to cognition at other spatial scales (i.e. vista, environmental, and geographical scales). This question should be examined in the future.

Conclusions

The influence of handedness on spatial abilities is a research field that has been relatively neglected. Many psychology studies only recruit right-handers, which only provides partial answers to many questions. The results in the current study indicate that, for mixed-handed people, embodied experience is important in the mental rotation of hands and the information is processed underlying a visual-proprioceptive integration cognitive mechanism. Nevertheless, for extreme-handed people, the results only showed that extreme right-handers had an overall better performance than extreme left-handers. The findings suggest that world knowledge might independently influence performance for left hand stimuli while the performance for right hand stimuli is influenced by a combination of world knowledge and embodied experience. More importantly, this study provides a new approach to compare the influence of embodied experience and world knowledge in spatial tasks.

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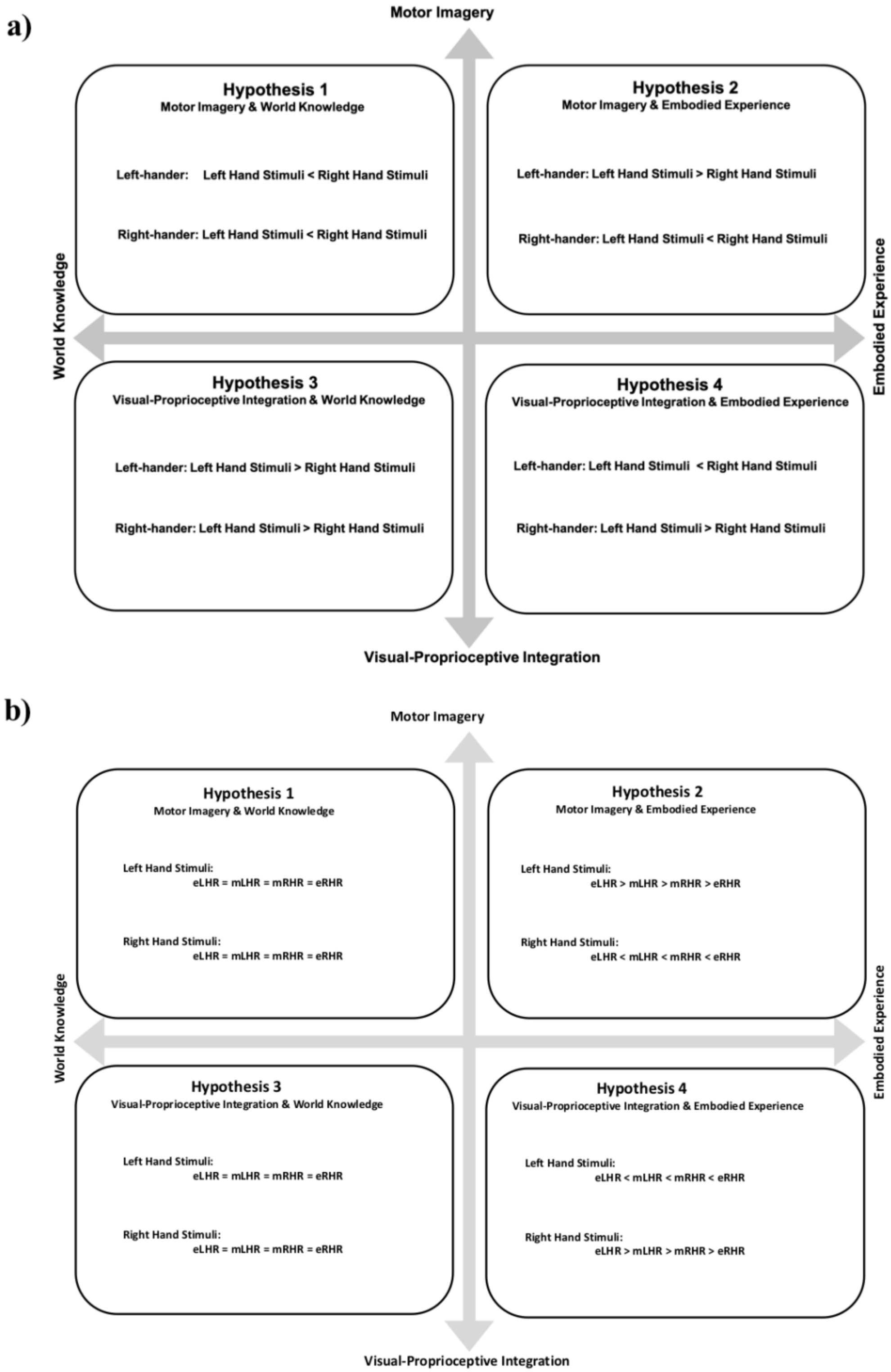

Figure 1. Hypotheses and predictions. a) Predictions based on categories of subject's handedness. b) Predictions based on categories of hand stimuli tested. eLHR = extreme left-handers; mLHR = mixed left-handers; eRHR = extreme right-handers; mRHR = mixed right-handers.

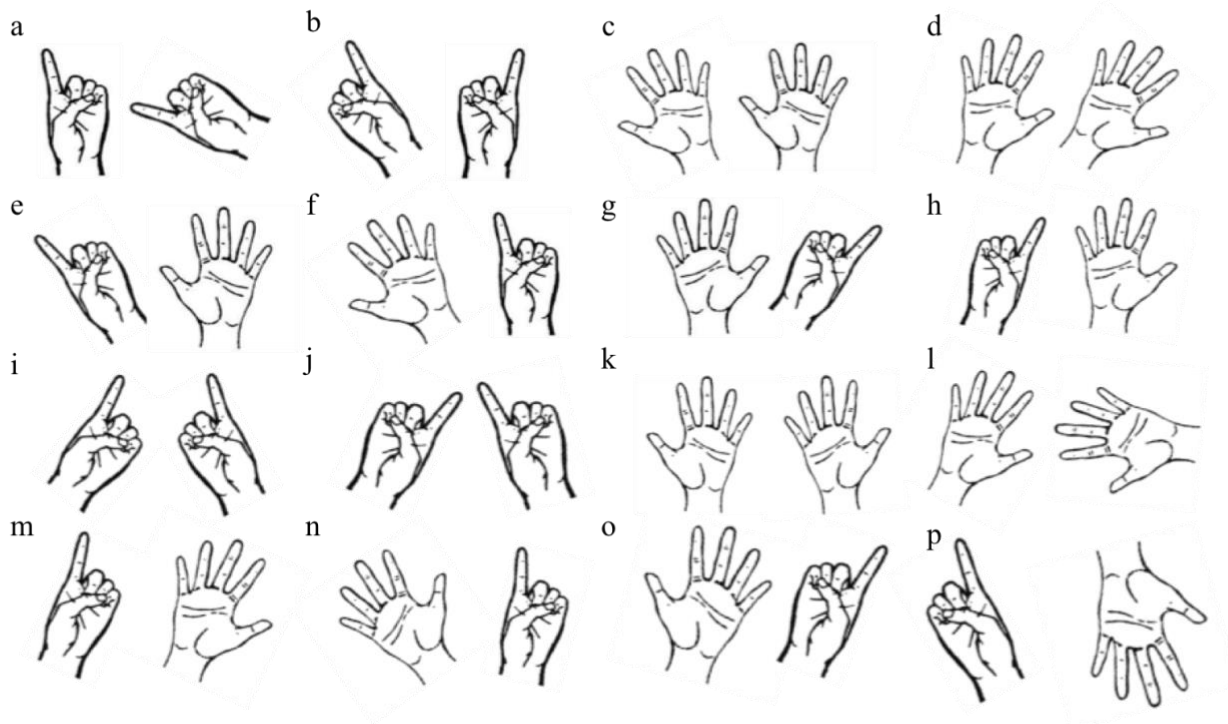

Figure 2. All hand stimuli combinations. The same hand condition (a – h) includes 10 pairs each: (a) left pointer pairs, (b) right pointer pairs, (c) left palm pairs, (d) right palm pairs, (e) left pointer left palm pairs (pointer on the left), (f) left palm left pointer pairs (palm on the left), (g) right palm right pointer pairs (palm on the left), (h) right pointer right palm pairs (pointer on the left). The different hand includes (i – p) includes 10 pairs each: (i) left pointer right pointer pairs (left pointer on the left), (j) right pointer left pointer pairs (right pointer on the left), (k) left palm right palm pairs (left palm on the left), (l) right palm left palm pairs (right palm on the left), (m) left pointer right palm pairs (left pointer on the left), (n) right palm left pointer pairs (right palm on the left), (o) left palm right pointer pairs (left palm on the left), and (p) right pointer left palm pairs (right pointer on the left).

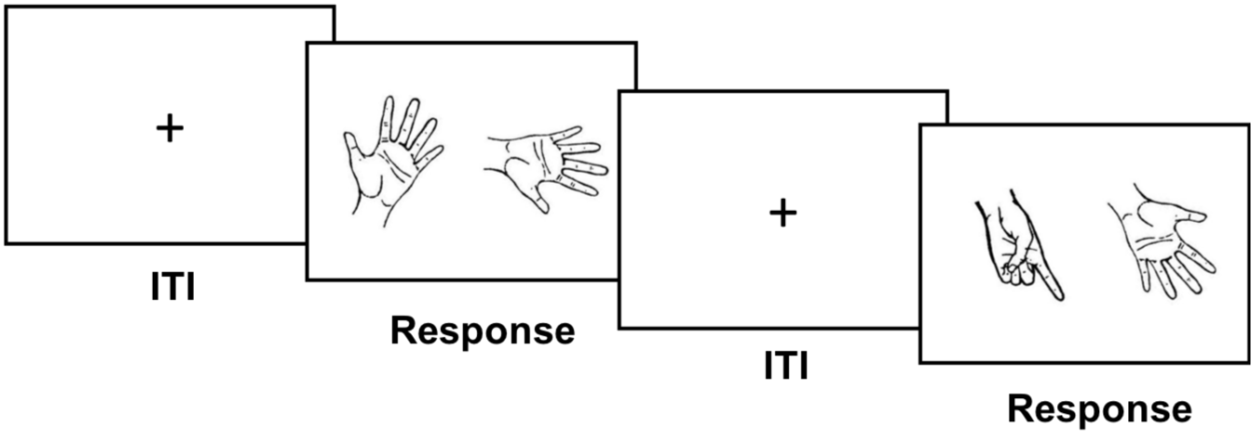

Figure 3. The flow of two trials. The ITI is 1000 ms. During the response, the task of the participant is to decide whether the two hand stimuli are the same hand or different hands.

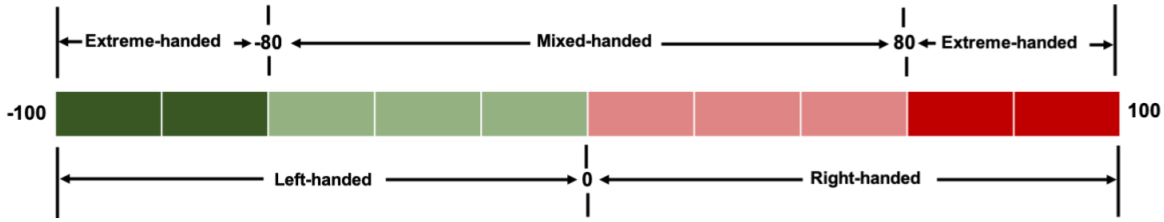

Figure 4. Handedness categorization measured by the Edinburgh Handedness Inventory. For handedness direction, if the laterality quotient (LQ) score was within the range of -1 to -100, then the subject was considered left-handed. If the LQ score was within the range of +1 to +100, then subject was considered right-handed. For handedness strength, if the LQ score was between -80 to +80, then the handedness strength was mixed. If the LQ score fell in ranges of either -100 to -80 or +80 to +100, then the handedness strength was assigned as extreme.

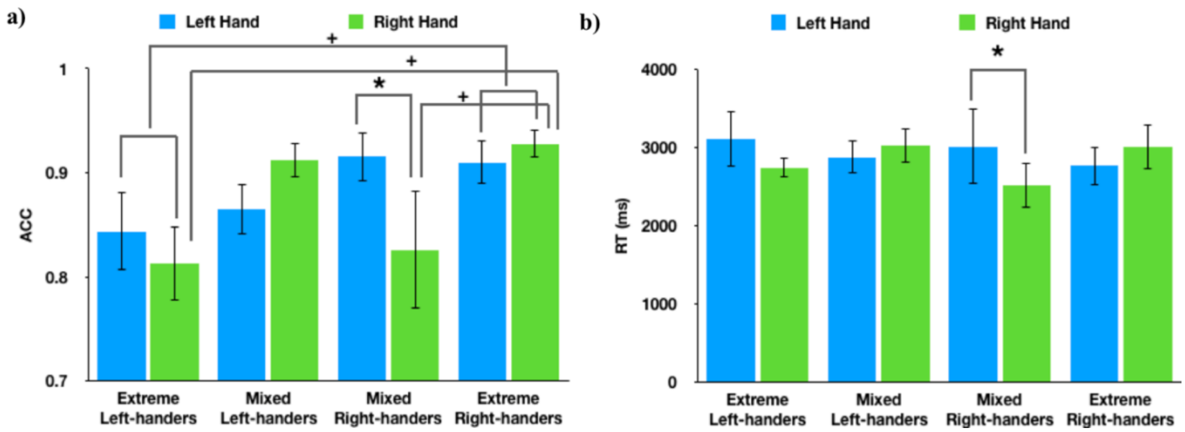

Figure 5. Performance for same hand stimuli/same gesture trials. Significance levels labeled in the figure is only based on the *handedness direction x handedness strength x hand stimuli tested* 3-way ANOVA among all subjects. a). Accuracy for same hand stimuli/same gesture trials. Mixed right-handers had significantly higher accuracy for left hand stimuli than for right hand stimuli (supports Hypothesis 3 or 4). Extreme right-hander's accuracy was marginally higher than extreme left-handers (does not support any hypotheses). Extreme right-handers had marginally higher accuracy than mixed right-handers and extreme left-handers for right hand stimuli (both support Hypothesis 2). In addition, mixed left-handers had a higher accuracy tendency for right hand stimuli than for left hand stimuli (supports Hypothesis 1 or 4). Mixed left-handers also had higher accuracy tendency for right hand stimuli than mixed right-handers (supports Hypothesis 4). b) Reaction time for same hand stimuli/same gesture trials. Mixed right-handers responded faster for right hands than for left hands (supports Hypothesis 1 or 2). ACC = accuracy; RT = reaction time; + $p < 0.1$; * $p < 0.05$.

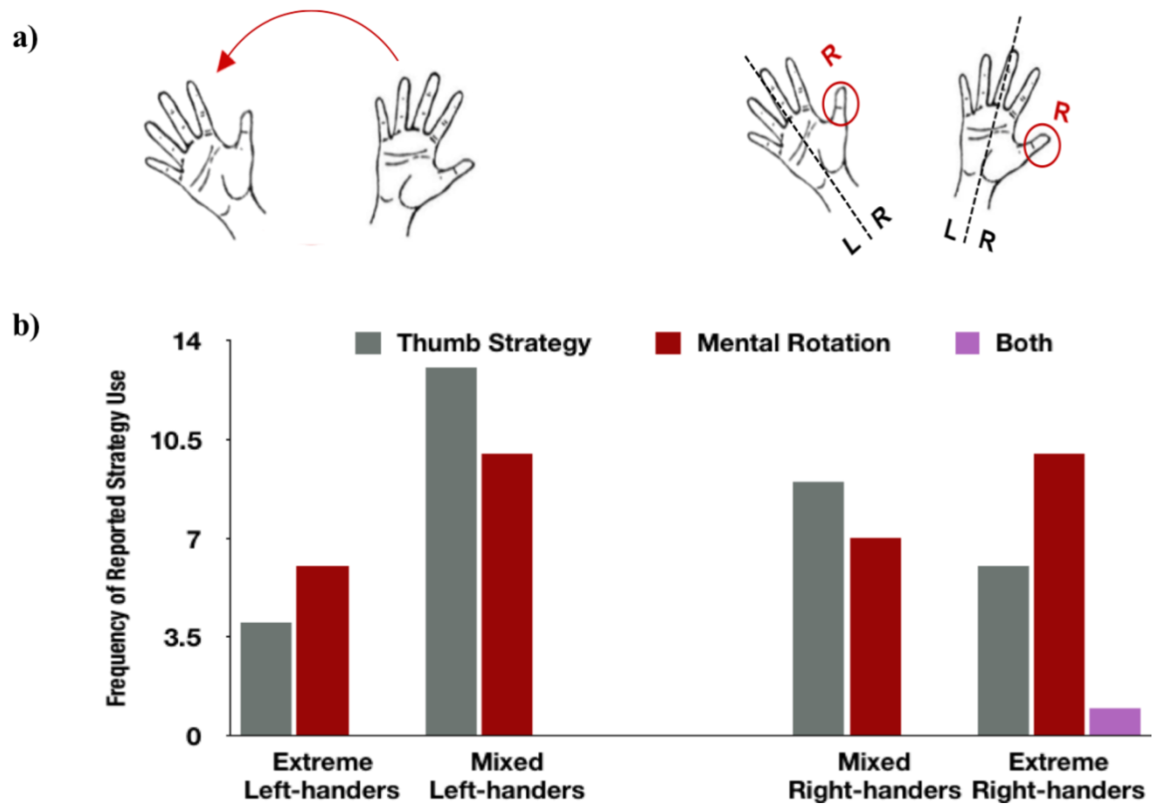

Figure 6. a) Strategies used in the mental rotation of hands. The mental rotation strategy is to mentally rotate one hand to a certain angle to align it with the other hand. The thumb strategy is to compare the relative position of the thumb on each hand. L = to the left of the hand central axis line. R = to the right of the hand central axis line. b) Frequency of reported strategy use. I found no group differences or interactions in strategy use.

Appendix

Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities by putting + in the appropriate column. Where the preference is so strong that you would never try to use the other hand unless absolutely forced to, put + +. If in any cases you are really indifferent put + in both columns.

Some of the activities require both hands. In these cases the part of the task, or object, for which hand preference is wanted is indicated in brackets.

Please try to answer all the questions, and only leave a blank if you have no experience at all of the object or task.

		Left	Right
1	Writing		
2	Drawing		
3	Throwing		
4	Scissors		
5	Toothbrush		
6	Knife (without fork)		
7	Spoon		
8	Broom (upperhand)		
9	Striking Match (match)		
10	Opening box (lid)		
i	Which foot do you prefer to kick with?		
ii	Which eye do you use when using only one?		