SISSA
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Neuroscience Area – PhD course in
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# Visuo-spatial reasoning in the human brain

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# Abstract

This thesis explores the brain correlates and contextual factors influencing visuo-spatial reasoning through Mental Rotation (MR) tasks in men and women. Visuo-spatial reasoning, a critical cognitive function, underpins everyday activities and is often assessed through MR tasks, where previous studies have shown gender differences favoring men. The research addresses the ongoing nature-nurture debate by examining the contributions of top-down (strategy-related), bottom-up (stimulus-related), and cognitive traits to MR performance and neural activation. Four experiments are conducted to: (1) investigate gender-specific strategy preferences in MR tasks; (2) characterize the neural correlates of MR and their modulation by imagery strategies; (3) compare brain activations related to different MR stimuli (abstract, manipulable, and bodily); and (4) assess the impact of individual cognitive traits on MR performance and brain activity. This comprehensive approach aims to provide deeper insights into the cognitive and neural mechanisms underlying gender differences in MR, with implications for understanding disparities in STEM-related fields.

# Contents

# Chapter 1

# General introduction

## 1.1 Gender differences in mental rotation

Visuo-spatial reasoning permeates our daily life. Actions like parking our car, finding our way to the bakery, or entering doors strongly rely on our ability to extract relevant information from the environment [for example the mental snapshot of our car] and mentally transform it [e.g. imagining whether our car fits the actual parking lot], in order to estimate or predict the outcome of an eventual action [e.g. maneuvering our car to enter the parking lot]. Generally speaking, spatial ability is the capacity to comprehend the connections between various locations in space or the ability to visualize the movements of two- and three-dimensional objects (Clements et al., 2003; Wang et al., 2014). In experimental settings, one way to objectively measure visuo-spatial reasoning is offered by the so-called Mental Rotation (MR) tasks. MR occurs when imagining how an object would look like if seen from a different viewpoint (Shepard & Metzler, 1971; Shepard & Cooper, 1986) and constitutes a critical ingredient in the conceptualization of spatial intelligence. Previous behavioral studies showed that men are more accurate and faster than women, especially when MR concerns three-dimensional abstract objects (see Figure 1) (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971; Voyer et al., 1995; Zapf et al., 2015). This pattern has been replicated in large cross-cultural samples (Peters et al., 2006; Silverman et al., 2007). As spatial skills have shown positive correlations with academic and career success in the Science, Technology, Engineering and Mathematics (STEM) disciplines (Shea et al., 2001), women's non optimal performance on MR tasks may partly account for the current underrepresentation of women in these areas (Ceci et al., 2009; Miller & Halpern, 2014).

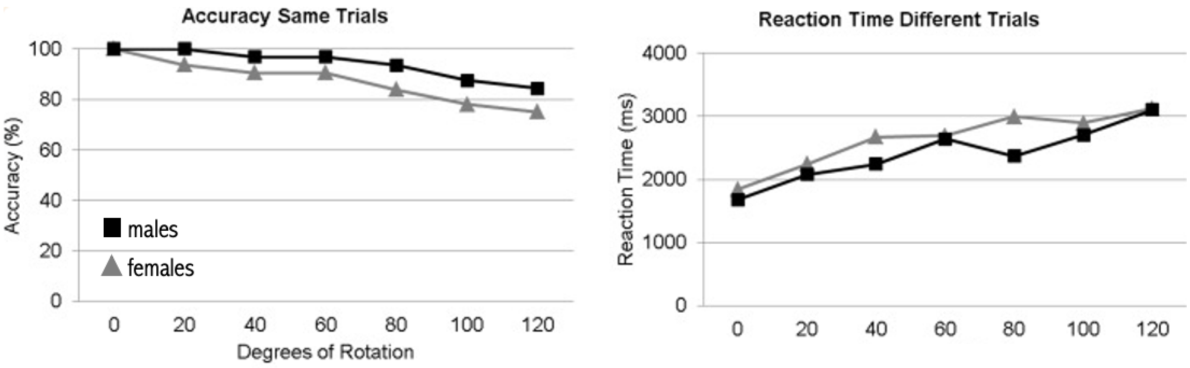

**Figure 1** – Psychometric patters according to the degree of rotation, separated for males (black squares) and females (grey triangles) (Adapted from Zapf et al., 2015). Females show a lower accuracy (left) compared to males as well as larger reaction times (right).

## 1.2 The nature-nurture debate

The factors that contribute to gender differences in MR are still poorly understood and subject to the nature/nurture debate. The nature-nurture debate about MR explores whether the ability to mentally rotate objects is primarily influenced by genetic and biological factors (nature) or by environmental and experiential factors (nurture). Proponents of the nature argument argue that MR is innate and largely determined by genetic factors. They point to evidence from studies showing that MR skills are present early in life and that there are consistent gender differences, suggesting a biological basis (Johnson & Moore, 2020; Moore & Johnson, 2020; Vuoksimaa et al., 2010).

On the other hand, advocates of the nurture perspective emphasize the role of experience and learning in developing MR skills. They argue that practice (De Lisi & Wolford, 2002; Feng et al., 2007; Roberts & Bell, 2000), education (Clements et al., 2003; Richardson, 1994), and cultural influences (Jansen et al., 2019; Janssen & Geiser, 2012; Nunez et al., 1998) significantly shape one's ability to perform mental rotations, highlighting that these skills can be improved with training and that differences among individuals and groups can be attributed to varying experiences and opportunities for spatial reasoning practice. Overall, the debate continues as researchers acknowledge that both genetic predispositions and environmental factors contribute to mental rotation abilities, with ongoing studies aiming to clarify the relative contributions of each.

## 1.3 Top-down influences

One possibility to account for gender differences is that men and women rely on different top-down imagery strategies to solve MR tasks. According to Zacks et al. (2000), MR tasks can be accomplished by using an object-based view (i.e., by taking the object itself as a reference frame) or an egocentric view (i.e., by taking the viewer's perspective as a reference frame). Object-based transformations are imagined rotations or translations of objects relative to the reference frame of the environment. Effector-based perspective transformations are imagined rotations or translations of one's point-of-view relative to that reference frame.

The link between the environmental reference frame, the intrinsic reference frames of objects in the environment, and the observer's effector-based reference frame is updated in both object-based transformations and effector-based viewpoint transformations. Nonetheless, the two transformations update distinct relationships. When an object undergoes object-based transformations, all of its relationships with its intrinsic coordinate frame are altered, but the relationships between the environmental and effector-based coordinate frames stay the same. When there are effector-based perspective transformations, each object's associations with the observer's effector-based coordinate frame are changed, but the relationships between the environmental coordinate frame and those of the objects in the environment are fixed.

The use of one or the other strategy would result in different psychometric patterns. In particular, when people use the object-based view (or visuospatial strategy), their Response Time (RTs) to the MR tasks are strongly correlated with the angular disparity between the current view of the target object to mentally rotate and its typical upright position or reference/target imagined position . On the other hand, when people use an effector-based view (or motor strategy), RTs reflect the biomechanical constraints mirroring those of the real movements that would be required to physically rotate the target object. This brings that movements oriented away from the midsagittal body plane (lateral movements) take longer than those oriented towards the midsagittal body plane (medial movements) (Papeo et al., 2012; Parsons, 1987b, 1987a, 1994; Zacks et al., 2000) (Figure 2). As shown by Wolbers et al. (Wolbers, 2003), strategies can be explicitly implemented and they trigger different MR networks. For example, the (effector-based) motor strategy can be imposed by a command such as: "Imagine that you turn the left figure with your hand until it matches the right figure" (Wolbers, 2003; Wraga et al., 2010). On the other hand, a visual (object-based) strategy can be imposed by telling participants: "Imagine that the figure is rotated on itself until it lines up with the other one" (Jordan et al., 2002; Wolbers, 2003).

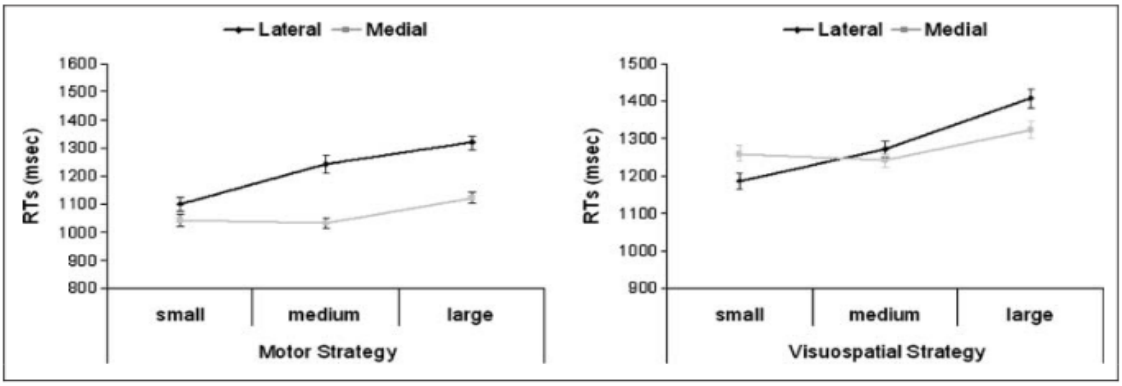

**Figure 2** – Different strategy-related psychometric patterns for mental rotation (Papeo et al., 2012). RT increases with the degree of rotation. In addition, in the motor strategy (left), the RT for mental rotations away from the midsagittal plane (Lateral, in black) are slower than those towards the midsagittal plane (Medial, in grey)..

A meta-analysis from 2016 (Tomasino & Gremese, 2016) revealed that the general MR network includes the inferior and superior parietal lobule bilaterally; left precentral gyrus; inferior frontal gyrus bilaterally; middle frontal gyrus bilaterally; supplementary motor area; left insula; inferior and middle occipital gyrus bilaterally, and cerebellum bilaterally. When using an object-based strategy, we usually observe predominant implications of occipital areas, as well as right temporal and parietal areas. When using an effector-based strategy we usually see in addition to the areas implicated in the object-based strategy, a predominant motor network activation, preferentially on the left sensorimotor area.

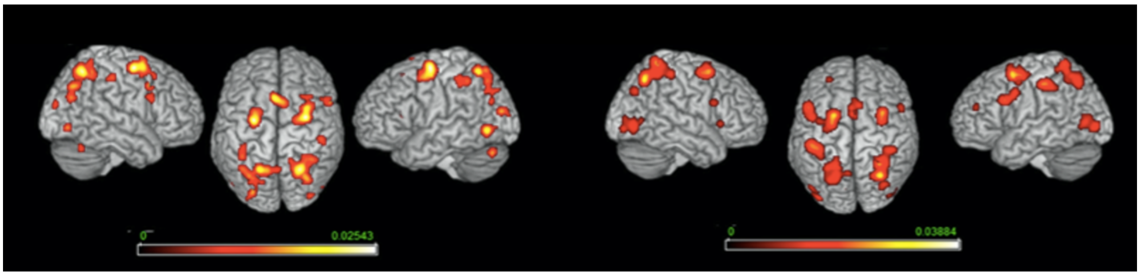

**Figure 3 –** Neural networks triggers by the use of an object-based strategy (left) and effector-based strategy (right) in mental rotations tasks. The object-based strategy triggers specifically the use of occipital areas, right temporal and parietal areas. The effector-based strategy triggers a motor network activation and the left sensorimotor area (Tomasino & Gremese, 2016).

MR-related brain imaging studies showed that deciding whether two 3D objects are identical or not is associated with the activation of different brain networks in men versus women. Men have shown to use a strong superior parietal activity, while women tend to recruit inferior frontal and temporal regions. This suggests that while males may be biased towards a visuospatial strategy, females are biased towards a motor strategy for the rotation of abstract objects (Hugdahl et al., 2006).

## 1.4 Bottum-up influences

In addition to the strategy, also the type of stimuli used for the MR task can induce the activation of different brain networks (bottom-up phenomenon). For example, mental transformations of bodily vs. non-bodily images are associated with different patterns of activation. A bilateral sensorimotor activation was found by comparing the bodily- to non-bodily stimuli. The network included the left inferior parietal lobe, right angular gyrus, left superior parietal lobe and right postcentral gyrus (Areas 2, 3b, and 4p), in addition to the left superior frontal gyrus and middle cingulate cortex. The reverse contrast (non-bodily related > bodily-related stimuli) included exclusively right-lateralized activations in the middle occipital gyrus, cuneus and superior parietal cortex (Aso et al., 2007; Tomasino & Gremese, 2016).

The literature on MR has shown that the key areas supporting MR of 3D cubes seem to be the superior parietal lobule (BA 7), together with the inferior frontal gyrus (BA

44/45) (Cohen et al., 1996; Thomsen, Hugdahl, Ersland, Barndon, Lundervold, Smievoll, & Roscher, 2000), the middle frontal gyrus (BA 8), the parieto-occipital border (BAs 39/19) (Cohen et al., 1996) or –as in (Richter et al., 2000)– the lateral premotor cortex (BA 6) and the supplementary motor area (medial BA 6). In addition, if the left hemisphere of the human brain is lesioned, the MR of images of body parts is impaired. While lesions in the right hemisphere impair MR of images of external objects (Tomasino & Rumiati, 2004). It's important to note that in the natural environment, MR tends to involve man-made objects, like tools or familiar objects.

Some studies have shown that spatial processing for everyday objects differs from that conventionally used in the laboratory. Grèzes and colleagues (2003) examined specifically how an object's intrinsic properties influenced motor responses that were either consistent with or inconsistent with the action the object permitted. Their research revealed faster motor responses to objects that permitted a steady hold. These changes were also demonstrated by imaging studies. For instance, Vingerhoets and colleagues (2002) discovered variations in how instruments and human hands were handled during magnetic resonance imaging. Pairs of tools only produced left premotor brain activity, whereas pairs of hands produced bilateral premotor activation. The results suggest that while participants envisioned using both hands in the hand condition, they pictured using their favorite hand—the right hand—to manage things in the tool condition. The covert actions of motor imagery appear to replicate the "natural way" that a person would manage the object in reality, and the activation of cortical regions during mental rotation appears to be driven, at least in part, by an internal mechanism that depends on the specific behaviors induced by the type of stimuli presented.

Studies on gender variations within stimulus categories abound. Jordan and colleagues (2002), for instance, demonstrated that women activated the inferior temporal gyrus (ITG) and dorsal premotor cortex (PMdc), the right superior parietal lobule (SPL), intraparietal sulcus (IPS), and the left inferior parietal lobule (IPL) and anterior IPS more than males did in an experiment combining several types of stimuli. Conversely, men showed more bilateral activation in the right posterior occipital sulcus (POS) and left posterior IPS of the primary motor cortex. In a subsequent study, gender differences were examined through a comparison of two stimulus categories: produced tools and human hands (Seurinck et al., 2004). The findings demonstrated that gender variations in hand rotation were restricted to women activating more left ventral regions and males appealing more to the lingual gyrus (Figure 4).

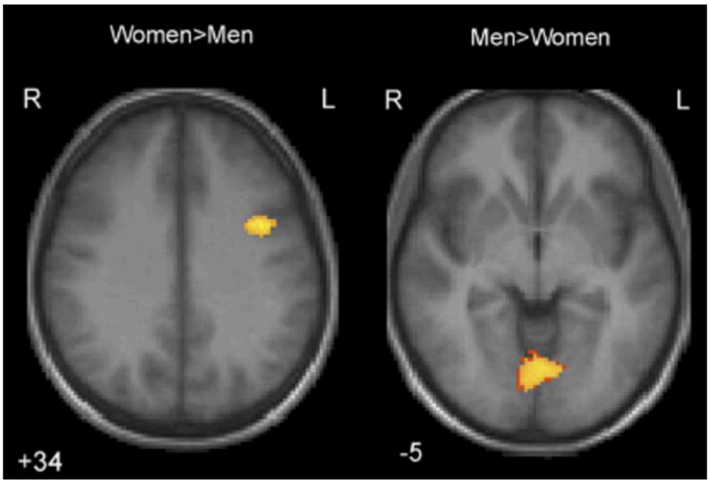

**Figure 4** – Patterns of activation for Women>Men (left) and Men>Women (right) in the Hand rotation condition. The Women>Men contrast reveals a cluster in the left ventral region, while the Men>Women contrast reveals a cluster in the lingual gyrus (Adapted from Seurinck et al. 2004).

## 1.5 The effect of testosterone

As far as the effects of nature are concerned, the hypotheses are more complicated to test. One potential candidate are sex hormones. Hormonal influences, shaped by both genetic factors and environmental conditions, are argued to play a significant role in spatial cognition (Geary, 1995, 1998). Testosterone is a key sex hormone crucial for sexual development and behavior, also present in brain regions linked to cognitive functions like language and spatial skills (Janowsky, 2006; Tapp et al., 2011). In average, men present higher levels of testosterone (10 to 38 nmol/L) compared to females (0.5 to 2.4 nmol/L). According to some evolutionary theories, testosterone contributes to the maintenance of spatial sex differences (Geary, 1995). Some explanations attribute the greater development of the neurocognitive basis of spatial ability, particularly in 3-dimensional contexts, to the fact that males have a greater evolutionary need for movement tracking and navigation than females have (Geary, 1995, 1998).

Various studies have explored the impact of testosterone on individual variations in spatial abilities within each sex. These studies have revealed positive correlations between higher testosterone levels, whether naturally occurring or administered externally, and improved performance in spatial tasks (Aleman et al., 2004; Burkitt et al., 2007; Cherrier et al., 2001; Slabbekoorn et al., 1999). For instance, research has shown that females with higher testosterone levels tend to outperform those with lower levels in tasks like visual maze navigation (Burkitt et al., 2007). Similarly, extraneous administration of testosterone has been linked to enhanced spatial ability performance in different demographics, including older men (Cherrier et al., 2001), female-to-male transgenders (Slabbekoorn et al., 1999), and young women (Aleman et al., 2004).

However, not all studies have consistently supported the association between elevated testosterone levels and enhanced spatial abilities, especially among females. Some research has found no significant correlation between testosterone levels and spatial task performance (Kubranská et al., 2014; Puts et al., 2010). Among males, the relationship between testosterone levels and spatial abilities has yielded mixed results, with some studies indicating a negative association between high testosterone levels and spatial skills (Christiansen & Knussmann, 1987; Hassler et al., 1992; Hromatko & Tadinac, 2006).

Furthermore, prenatal exposure to testosterone may influence cognitive development by affecting brain function and neural structure during early prenatal stages. Evidence from clinical samples, such as individuals with Congenital Adrenal Hyperplasia (CAH), suggests a potential link between elevated prenatal testosterone levels and improved spatial abilities in females (Berenbaum et al., 2012; Mueller et al., 2008). Nevertheless, the evidence regarding the role of prenatal testosterone in spatial abilities remains inconclusive, with some studies reporting null results or no significant differences in performance between individuals with CAH and control groups (Collaer & Hines, 2020; Malouf et al., 2006).

## 1.6 Cognitive traits

Beyond gender, strategy and stimuli, also individual cognitive traits can influence the performance in MR tasks. Cognitive traits are modes of acquiring and processing information which regulate an individual's cognitive functioning (Klein, 1951). They are stable through life and affect attitude, strategies, preferences, ways of perceiving and learning information (Jonassen & Grabowski, 1993). A first cognitive trait that plays an important role in MR tasks performance is the visual-verbal style (Kozhevnikov, 2007). The visual-verbal style is based on the dual-coding theory according to which information is processed and mentally represented in two ways: verbally and visually (Paivio, 1991). Visual-Verbal cognitive style therefore describes consistencies and preferences in processing visual versus verbal information. Mayer & Massa (2003), then define the "visualizer-verbalizer cognitive style" as thinking in pictures or words. People who tend to rely more on visual stimuli such as images (visualizers) can further be differentiate into spatial visualizers and object visualizers (Kozhevnikov et al., 2002). Spatial visualizers tend to be more comfortable handling spatially organized images, dealing with locations and spatial relationships among objects. Object visualizers would rather work with static images, and pay attention to shape, size, color and create vivid and manipulable images. Generally, they encounter difficulty in handling abstract stimuli and representations (Kozhevnikov et al., 2005). Some studies (Blajenkova et al., 2006; Kozhevnikov et al., 2005) showed that those two types of visualization are associated with measurable differences in MR tasks (Vandenberg & Kuse, 1978), in that spatial visualizers are more accurate and faster than object visualizers. Another cognitive trait that might influence the performance in MR tasks is perspective taking, which is the ability to understand how our effector-based view might differ from another viewpoint. Surtees and colleagues (2013) suggested that it reflects the ability to engage in MR. Therefore, the better the visual perspective taking, the better the performance in a MR task. Finally, considering that flexibility is the cognitive trait reflecting the ability to adapt our behavior and thinking in response to complex and novel situations (Ionescu, 2012), it might have an influence on MR performance. In this vein, it has been recently shown that male participants have higher strategy flexibility and score significantly better than females (Nazareth et al., 2019).

## 1.7 Aim of the thesis

Altogether, the general goal of my thesis is to better understand the brain correlates of top-down, bottom-up, and cognition-related contextual differences in the brain correlates of visuo-spatial reasoning through MR in healthy women and men. Even if some elements of response have been given to us by some papers cited above, we still lack information on the factors influencing performance in the MR skill. To our knowledge, no study has combined these factors in a single project to try to answer this question. Thus, this project stands out because of its thorough and in-depth investigation of the above-mentioned factors.

To this aim four experiments are foreseen. Experiment 1 – "Behaviour and design" is aimed at investigating whether men and women show different preferences in terms of strategy for solving a mental rotation, by implementing a new and reliable observational tool for assessing mental rotation performances across two strategy conditions. Experiment 2-"Strategy" is thought to characterize the brain correlates of MR and whether they are modulated by different imagery strategies (top-down processes). Experiment 3 – "Stimulus" focuses the influence of bottom-up factors, comparing adopted strategies and activated brain areas in association with MR of abstract objects / manipulable objects / bodily figures. Experiment 4 – "Mind" investigates whether individual cognitive traits affect the brain activity associated with MR tasks and/or influence the performance in MR tasks.

# Chapter 2

## Experiment 1:

## Understanding sex differences in mental rotation through the role of strategies

Manuscript submitted to the Journal of Experimental Psychology: Human Perception and Performance. All the materials related to this paper (stimuli, data, and code for data analysis) are publicly available at the following GitHub repository: https://github.com/nadiaBRS/Understanding-sex-differences-in-mental-rotation-through-the-role-of-strategies.

### 2.1 Abstract

In this study we investigated whether men and women show different preferences in terms of strategy for solving a mental rotation (MR) task, using a new and reliable observational tool. In the effector-based condition (EBS), participants had to imagine rotating the image on the screen with their hand, while in the object-based condition (OBS), participants had to mentally rotate the image until a red mark reached the side indicated by the index arrow. A sample of 58 participants (29 women) underwent two experimental conditions and one a control condition in which no specific strategy was imposed. Because sex hormones have been known to affect spatial abilities, salivary testosterone levels and digit ratio were measured in order to look into a possible connection with MR. The results showed gender differences in accuracy depending on the strategy condition. Specifically, men outperformed women in the control condition as well as in the OBS, but no differences were found in the EBS. Consistent with this pattern,

women were more accurate in the EBS compared to the control condition, whereas men’s accuracy remained stable. Measures of testosterone did not show any link with MR performance. The results suggest that men's and women's performance is differentially affected by the imposition of different MR strategies. We replicated some of the known results in the field: the man advantage in accuracy, and the differences in strategy, as well as the clear behavioral differences between conditions, showing that the implemented paradigm is effective in studying the phenomenon of MR.

## 2.2 Introduction

Mental rotation (MR) involves mentally rotating an object to understand its appearance after rotation without changing one's viewpoint. The classic design of MR tasks typically involves the simultaneous display of two or three dimensional line-drawings on the screen, with instructions to decide whether the images are congruent or incongruent. It has been hypothesized that, in order to complete the task, individuals form a mental image of one of the depicted drawings, and mentally rotate it to see if it can be brought into correspondence with the other picture (Shepard & Metzler, 1971). The behavioral results supported this idea: the time it took participants to decide whether the objects in a pair were the same or different increased in direct proportion to the angular rotation difference between them.

As far as gender differences are concerned, the 3D MR task consistently produces the most robust performance differences between men and women (Halpern, 2013; Linn & Petersen, 1985; Voyer et al., 1995), with men showing shorter reaction times and higher accuracy than women. Many hypotheses have been put forward to explain these differences, such as the influence of early environment (Baenninger & Newcombe, 1989; Connor et al., 1977), hobbies and activities (Feng et al., 2007; Nazareth et al., 2019) or sex hormones (Hausmann et al., 2000; van Hemmen et al., 2016). Our daily activities can have an impact on our cognition, and sometimes act as training for some of our abilities. Nazareth and colleagues (2013) have highlighted how stereotypically spatial activities undertaken during adolescence can have an impact on spatial cognition. For example, video games have sometimes been cited as improving our spatial skills (Feng et al., 2007; Podlogar & Podlesek, 2022; Spence & Feng, 2010). In particular, Feng and colleagues (2007) investigated the effect of a first-person shooter (FPS) video game on spatial attention and MR. Their results showed that after about 10 hours of training, gender differences in spatial attention were eliminated and differences in the MR task were significantly reduced. Furthermore, women benefited more than men from this effect. Although this example is not exhaustive, it is safe to say that both upbringing and training influence our cognitive abilities.

Gender-related differences in MR may also be influenced by genetic and hormone exposure variability that impacts spatial aptitudes. The connections between congenital adrenal hyperplasia and spatial skills lend credence to this idea. This syndrome is characterized by an excess of adrenal androgen production due to an enzyme deficiency that redirects cortisol precursors to the androgen pathway (Pang et al., 1980). Contradictory results have surfaced on the topic (Helleday et al., 1994; Malouf et al., 2006; McGuire et al., 1975). While some studies report masculinized spatial abilities in women (Hampson et al., 1998; Hines et al., 2003; Resnick et al., 1986), other report poorer spatial abilities in affected men (Hampson et al., 1998; Hines et al., 2003). Finally, other studies failed to report such differences at all (Gordon & Lee, 1993; McGuire et al., 1975; Puts et al., 2010; Resnick et al., 1986). It's worth noting that another strand of the literature suggests that the relationship between testosterone and spatial skills is more U-shaped than linear (Courvoisier et al., 2013; Moffat & Hampson, 1996; O'Connor et al., 2001). According to this model, moderate levels of testosterone may improve spatial cognition, while high levels may worsen it. The discrepancy in findings across studies on testosterone and spatial skills may be explained by the observed inverted U-shaped association.

Another unexplored potential factor that could explain the gender gap is the strategy used to solve the task. According to Zacks & Michelon (2005), the mechanisms differ depending on the reference used for the rotation. MR can be performed using an object-based perspective (i.e., using the objects itself as a frame of reference) or an effector-based perspective (i.e., using the observer's perspective as a reference frame). The use of the object-based strategy triggers the activation of parietal areas, whereas the effector-based strategy engages frontal and temporal areas (Papeo et al., 2012). As the object-based strategy has been shown to be faster and more accurate, while the effector-based strategy is slower and less efficient (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971), the observed gender difference could be explained by the individuals of the two sexes spontaneously using different strategies. Thus, men's higher performance might be explained by their spontaneous selection of an object-based strategy to solve MR, whereas women might spontaneously rely on the effector-based strategy.

As shown by Wolbers and colleagues (2003), strategies can be explicitly implemented and they trigger different MR networks. For example, the effector-based (i.e., motor) strategy can be imposed by a command such as: "Imagine turning the left image with your hand until it matches the right image" (Wolbers, 2003; Wraga et al., 2010). On the other hand, the object-based (i.e., visual) strategy can be imposed by telling participants: "Imagine that the image is rotated on itself until it is aligned with the other one" (Jordan et al., 2002; Wolbers, 2003). To dissociate the two MR strategies, Tomasino & Rumiati (2013) used explicit instructions with brain lesioned patients for the two MR conditions. In the motor condition, they were asked to imagine grasping the Shepard and Metzler stimulus with their left hand and rotating it in order to align this stimulus with the orientation indicated by the target cube. In the visual condition, the same stimulus pairs were presented, but the rotated cube contained a red square on its left or right side. Patients had to decide on which side of the cube (left or right) the red square was located. The results showed that patients with left hemisphere lesions showed a selective deficit in MR as a result of their manual activity, regardless of the type of stimulus, whereas patients with right hemisphere lesions were found to be impaired in MR through the use of a visual strategy. They concluded that MR can be achieved by recruiting different strategies supported by independent brain networks, and that these can be implicitly triggered or prompted at will.

These and similar paradigms were then used in fMRI studies to investigate the brain networks involved in MR. These networks have typically involved the following areas: (i) inferior and superior parietal lobule bilaterally; (ii) left precentral gyrus; (iii) inferior frontal gyrus bilaterally; (iii) middle frontal gyrus bilaterally; (iv) SMA; (v) left insula; (vi) inferior and middle occipital gyrus bilaterally, and (vii) cerebellum bilaterally (for a meta-analysis, see Tomasino & Gremese, 2016). The potential problem with such a design is that the areas associated with these activations may not be exclusively due to the MR. The fact that both images remain visible on the screen throughout the MR tasks triggers the activation of basic visual areas such as V1, but also that of other secondary areas responsible for processing geometric or color features. In addition, other executive functions come into play, provoked by ocular saccades to switch and compare one image with the other, resulting in the activation of frontal areas (for a review, see Pierrot-Deseilligny et al., 2003).

How can we dissociate the functional activations due to the MR from other mental processes? The design proposed in this study aims at isolating the MR process in a more optimal way. Instead of displaying two images on screen, we opted for a serial approach (see Christophel et al., 2015; Griksiene et al., 2019; Lamm et al., 2007), in which the target image appears after the one to be rotated. In between the two, a blank screen of a fixed duration allows the subject to perform MR without any other distraction. In order to validate the paradigm, we will conduct a the behavioral-only experiment to ensure that our results are consistent with those in the literature, both in terms of gender performance and strategy performance.

The method developed here partially adopts the design of Tomasino & Rumiati (2013), while presenting the serial features used by Christophel and colleagues (2015) in order to isolate the rotation phase from other processes. Should we be able to replicate the results in terms of gender differences and those resulting from the implementation of different strategies, we could conclude that the newly designed approach is reliable. This paradigm would then be transferred to fMRI, allowing us to investigate the functional gender differences in the use of different strategies for solving of MR tasks.

Thus, the aim of this study was twofold: first, we wanted to test whether the imposition of different strategies changed MR performance differently in men and women; in particular, we predicted that men would outperform women in the control condition and in the object-based conditions, whereas women' performance would be affected by the triggered strategy. Second, by using a serial design, we aimed to assess the stability of psychometric patterns commonly observed in MR tasks and to confirm the suitability of the design for future fMRI studies. In addition, we included a baseline (i.e., control) condition, in which no strategy was imposed and participants were free to choose their spontaneous method of MR resolution. This allowed us to compare the psychometric patterns between the control condition and the two experimental conditions, and to observe changes in the behavior from the spontaneous strategy they naturally adopt to that imposed by the task, which we expect to differ for men and women.

## 2.3 Methods

Data were collected in 2021. An a-priori power analysis run using G*power version 3.1.9.6 (Faul et al., 2007) showed that n = 42 was large enough to detect an effect of f = 0.2 at p < .05, for an ANOVA with 2 groups and repeated measured within factors using F-tests. Therefore, testing 60 participants seemed adequate, especially in light of similar behavioral studies (Cheung et al., 2009; Geisen et al., 2024; Tang et al., 2023).

### *2.3.1 Participants*

Sixty participants (30 women) aged between 18 and 35 were recruited via the local online platform. Two subjects (one man and one woman) were excluded due to the expression of a performance at chance level, yielding a final sample of fifty-height participants (29 women, mean age 23.93, SD= 3.17, range 19-31, and 29 men, mean age 26.55, SD=3.81, range 20-35). Prior to the experiment, each participant self-reported their perceived gender using a questionnaire, in light of the possible distinctions between biological sex and perceived gender (Wierenga et al., 2024). According to the questionnaire, every participant's perceived gender identity and biological sex were in agreement. Exclusion criteria for participating in the study were any form of neurologic or psychiatric disorder and left-handedness. All participants gave written informed consent prior to their participation in the study and received 15 euros for their participation. The study was approved by the local Ethics Committee and was conducted according to the guidelines of the Declaration of Helsinki (2013).

### *2.3.2 Procedure*

Subjects were shown 60 pairs of 3D drawings presented consecutively. Five images were drawn from the dataset developed by Shepard and Metzler (1971). Trials would begin with a screen displaying a fixation cross lasting 1 second. The first rotated image was then presented for 800 ms, tailed by a blank screen with a duration of 3 seconds. A cue would then appear for 500 ms, followed by a blank screen of 3 seconds. Finally, the second image was shown into its vertical position for 4.5 seconds. According to data gathered during the study's pilot phase, each image had an intuitive vertical that was primarily indicated by its longer arms. About forty participants were asked to rate the verticality of thirty Shepard & Metzler figures during the pilot. The figures we chose for the experiment were then limited to those that were deemed vertical by the majority of the evaluators.

The stimuli were presented in three blocks of 20 trials per condition. Between each block, a short break would allow participants to rest. A total of 10 rotation angles were possible, ±30°, ±60°, ±90°, ±120° and ±150°. The set of 60 pairs was selected randomly from the larger set, with the restriction that all 5 shapes and 10 rotation angles be presented for each of them.

In the control condition (Figure 1), the cue consisted of circular arrows, showing the direction of the rotation to be made (clockwise or counterclockwise in the picture-plane). The instructions were the following: "Look at the first image, then the cue. Mentally rotate the first image in the direction indicated by the cue, until the image is in its vertical position. Then compare the second image appearing on the screen with the result of your MR, and indicate whether it is the same or different.” To answer, participants had to press given keys on the computer keyboard.

In the effector-based condition (EBS, Figure 2), the cue was replaced by a human right hand, pointing left or right. The participants were directed to visualize placing their own hand in the position indicated by the cue, grasping image 1, and mentally rotating it to its vertical position in accordance with the hand's natural motion. Consequently, the movement that needed to be done was counterclockwise if the hand pointed to the right and clockwise if it pointed to the left. The purpose of the explicit request to use the right hand was to frame the viewer's perspective and initiate an effector-based, or motor, strategy.

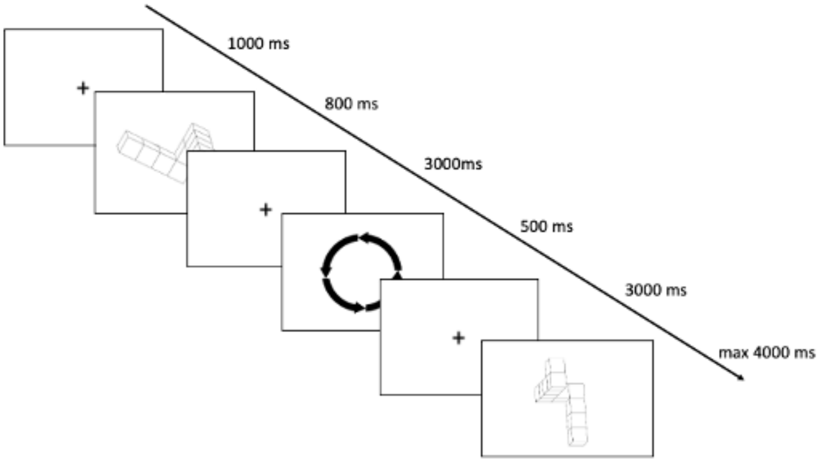

**Figure 1 – Example trial in the control condition**. In this condition, subjects were asked to mentally rotate the first image in the direction given by the arrows until reaching the vertical position. When presented with the second image, participants had to answer if it was congruent or incongruent with the instruction given. In the example, the trial is congruent.

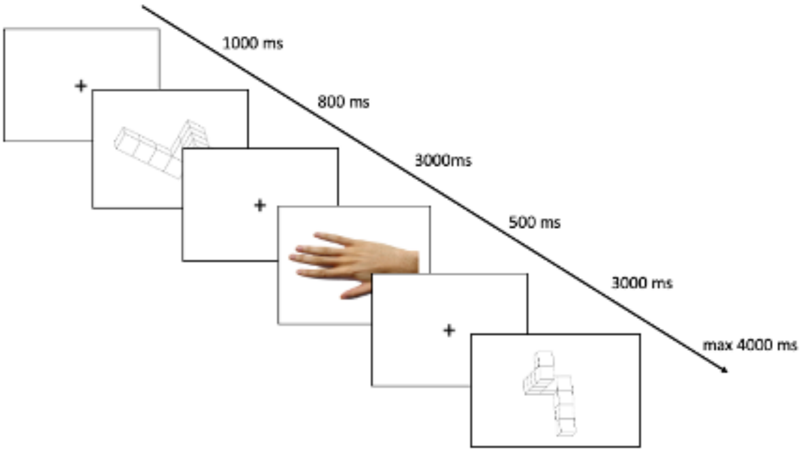

**Figure 2 – Example trial in the effector-based condition.** Subjects were asked to mentally rotate the first image in the direction by the hand until reaching the vertical position, following the natural movement of a human right hand. When presented with the second image, participants had to answer if it was congruent or incongruent with the instruction given. In the example, the trial is incongruent.

In the object-based strategy (OBS) condition (Figure 3), the first image had a red mark on one of its sides. A horizontal arrow pointing left or right served as the cue. To place the red mark on the side indicated by the arrow, participants had to mentally rotate the image in the picture-plane until it reached the vertical position. Under these circumstances, the cue was indicating the side where the mark should be in the final position rather than the direction of rotation. On the second image, the red mark was not shown. The purpose of the red mark was to force an object-based spatial strategy, forcing the object itself to be the frame of reference.

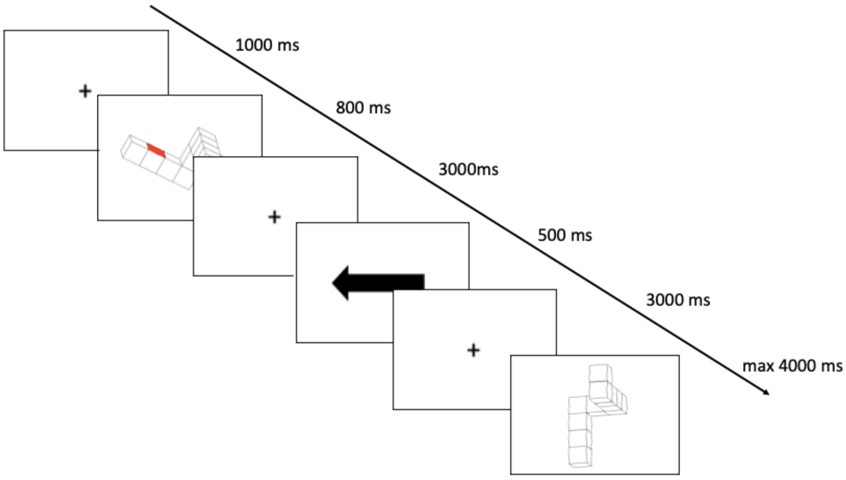

**Figure 3 – Example trial in the object-based condition**. Subjects were asked to mentally rotate the first image in the picture-plane, in such a way that the red mark would end up on the face indicated by the direction of the arrow. When presented with the second image, participants had to answer if it was congruent or incongruent with the instruction given. In the example, the trial is incongruent.

For all three conditions, in 50% of the cases, the answer was "congruent" (like in Figure 1), and in 50% of the cases, the answer was "incongruent". To add some difficulty, the "incongruent" answers were divided into 2 categories: "wrong rotation" (like in Figure 2) or "mirrored" (like in Figure 3), to avoid memorization of the mirrored images. All participants started the experiment with the control condition. The experimental conditions (i.e., effector-based condition and object-based condition) were presented in a counterbalanced order.

### *2.3.3 Additional measures*

Saliva was tested for free testosterone, which is a measure of the physiologically accessible portion of testosterone in the bloodstream (Rilling et al., 1996). Participants were asked to provide a sample, which consisted of at least two milliliters of saliva poured into a plastic tube, prior to the experiment. After that, samples were kept at -20 degrees until they were brought to the analysis lab, where they underwent instant analysis. Testosterone levels were measured with an enzyme-linked immunosorbent assay (ELISA) protocol (manufactured by IBL International GmbH, Germany). The assay sensitivity was 29,8 pmol/. The average intra-assay coefficient of variation was 5.6% and inter-assay imprecision was 8.7%. Regarding prenatal testosterone, the fingertip to the middle of the basal crease on the hand's palm was used to measure the lengths of the second (index finger) and fourth (ring) fingers. These numbers are divided to get the 2D:4D ratio (Brown et al., 2002). Because men and women show an important difference in testosterone measures, those analyses were done separately for each group.

As mentioned in the introduction, FPS video games can have a training effect for MR. To account for this effect, a questionnaire was given to participants to assess the amount of potential training they benefited during their lives. By the same token, we wanted to check whether overall performance improves with each block. As mentioned earlier, men and women benefit differentially from training on a spatial task. Thus, we also added block as a factor to our ANOVAs to investigate a potential impact on accuracy or reaction time.

### *2.3.4 Data analysis*

Anticipations (RT < 200 ms), missed responses and errors were discarded from RTs analysis. Statistical analyses were performed with RStudio (https://rstudio.com/). Our main hypotheses of gender differences across MR strategies were additionally investigated by contrasting in a pairwise manner condition|gender and gender|condition (library ’emmeans’) for the planned comparisons as specified in the Introduction section.

Additionally, accuracy and RTs were assessed with a three-way analysis of variance (ANOVA) including Gender (men, women) as a between-subjects factor and Condition (control, object-based and effector-based) and Block order (first, second, third) as the within-subject factors. Also, we checked if the amount of hours spent playing video games had an effect on MR performance (i.e., accuracy and RTs) with a two-way ANCOVA using hours of video games played on average per week as a continuous factor, and condition as a categorical factor. Three-way ANCOVAs were also computed to analyze accuracy and RTs with salivary testosterone, digit ratio and condition as main factors. Main effects and interactions were considered significant according to a level of significance of .05. As effect size estimates of the main effects and interactions, we computed the η2 (library 'effectsize') for linear mixed models. Additionally, to investigate a potential non-linear relationship between free testosterone and performance (accuracy and reaction time), we ran quadratic regressions to verify that a possible U-shaped relationship did not exist.

## 2.4 Results

### *2.4.1 Behavioral results*

The ANOVA results for accuracy revealed a main effect of Gender [*F*(1,56) = 5.404, *p*=.024, ηp2=0.09], showing that males overall outperformed females (see Table 1). The interaction between Gender and Condition did not reach significance [*F*(2,448) = 1.84, *p*=.15, ηp2<0.001]. Planned comparisons t-tests, testing specifically our condition|gender and gender|condition hypotheses as stated in the introduction, revealed significant gender differences in the control condition [*t*(1,56) = -2.76, *p*=.008, *d*=-0.63], as well as in the OBS condition [t(1,56) = -2.19, p=.032, *d*=-0.45], where men showed higher accuracy than women. In the EBS condition however, the difference didn't reach significance [*t*(1,56)=-1.40, *p*=0.164, *d*=-0.29] (see Figure 4).

**Table 1**. Mean accuracy and reaction time for men and women, across all conditions.

| | **Accuracy (Mean ± SD)** | | | **RTs (Mean +- SD)** | | |
|---|---|---|---|---|---|---|
| **Condition** | control | OBS | EBS | control | OBS | EBS |
| **Men** | 0.82 ± 0.11 | 0.83 ± 0.14 | 0.83 ± 0.12 | 1.36 ± 0.37 | 1.22 ± 0.39 | 1.14 ±- 0.35 |
| **Women** | 0.72 ± 0.11 | 0.75 ± 0.11 | 0.76 ± 0.14 | 1.35 ± 0.27 | 1.24 ± 0.3 | 1.20 ±- 0.3 |

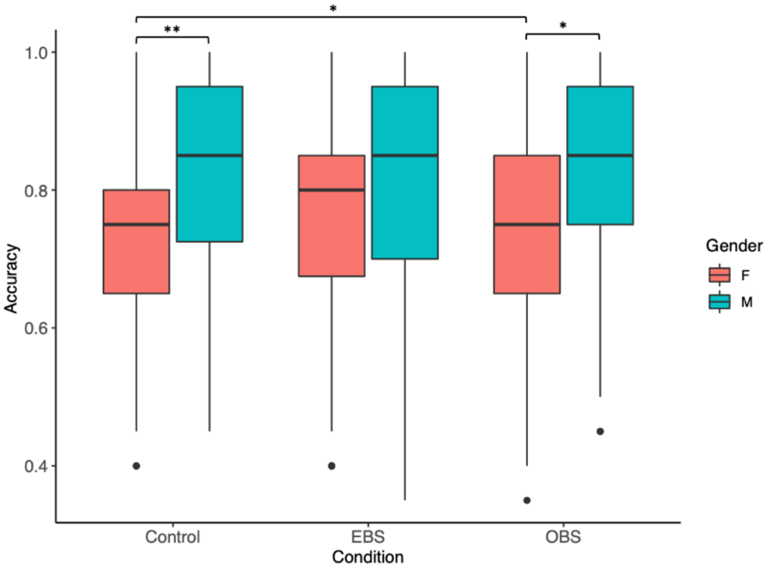

**Figure 4 – Accuracy across conditions for both groups.** Paired comparisons with t-tests (corrected for Tukey) revealed significant differences within the OBS and control condition. For women, significant differences were found between the EBS and control conditions. Men didn't present any differences across conditions. *Notes a significant different p < 0.05. **Notes a significant different p < 0.01.

Within females, planned comparisons t-tests showed higher accuracy when adopting the EBS with respect to the control condition [*t*(448)=-2.311, *p*=.02]. Males on the other hand didn't show any differences in accuracy between conditions.

The ANOVA also showed a significant interaction between condition and block [*F*(1,448) = 3.643 , *p*=0.006, *ηp2*=0.03]. However, comparing different blocks through post-hoc tests failed to highlight any significant differences (see figure 5).

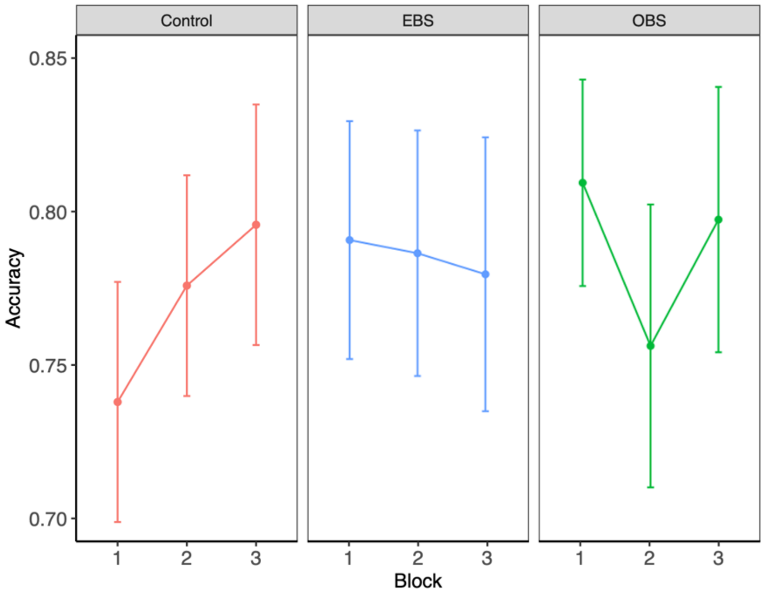

**Figure 5 – Interaction between block and condition on accuracy.** Control condition is shown in red; effector-based strategy (EBS) is shown in blue; object-based strategy (OBS) is shown in green.

Regarding reaction times, behavioral results showed a significant effect of condition [*F*(2,448)=36.207, *p*<.001, *ηp2*=0.14], with the control condition taking significantly more time than the EBS condition [*t*(1,113)=2.95, *p*=0.003] (Figure 6).

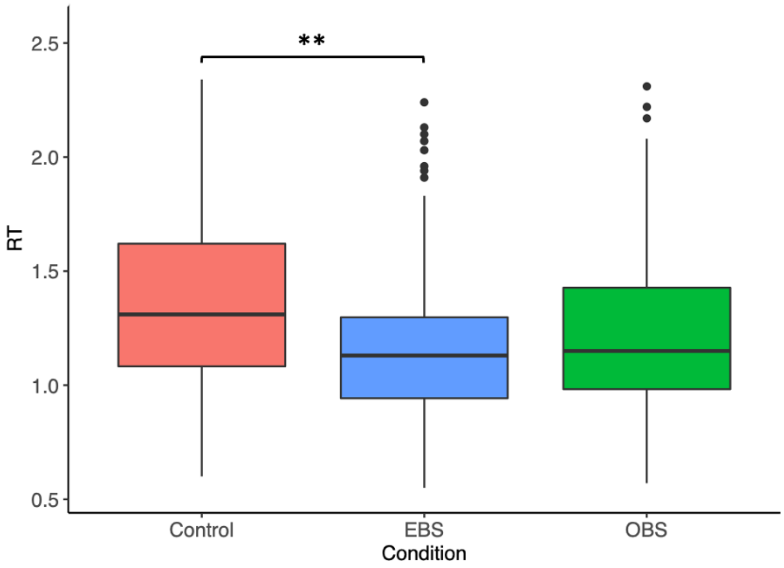

**Figure 6 – Reaction times across conditions for both groups**. Reaction times across conditions for both groups. Control condition is shown in red; effector-based

strategy (EBS) is shown in blue; object-based strategy (OBS) is shown in green. Paired comparisons with t-tests (corrected for Tukey) revealed significant differences between the EBS condition and the control condition. **Notes a significant different p < 0.01.

A main effect of block was also found, [*F*(2,448)=6.57, *p*=.001, *ηp2*=0.03], as well as a significant interaction condition*block [*F*(4,448)=3.01, *p*=0.01, *ηp2*=0.03] (Figure 7). When comparing different blocks with post-hoc tests however, no significant differences arose.

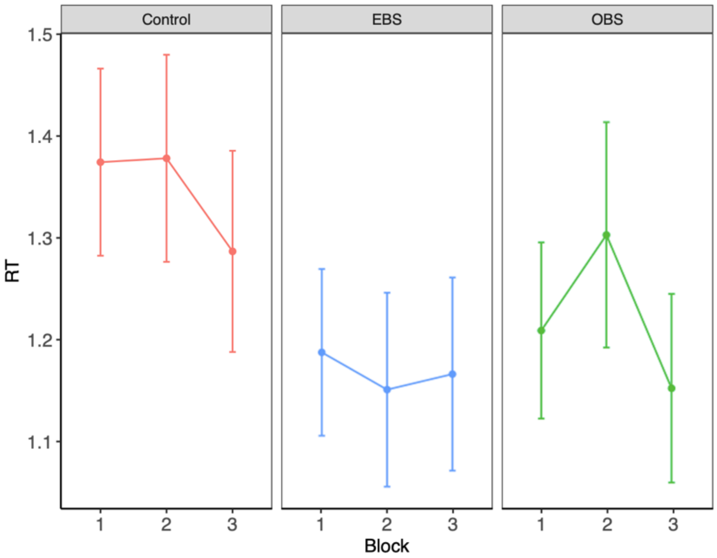

**Figure 7 – Interaction between block and on reaction times.** Control condition is shown in red; effector-based strategy (EBS) is shown in blue; object-based strategy (OBS) is shown in green.

### *2.4.2 Effect of videogames*

No beneficial effect was found for video games on MR performance. The mean amount of FPS video games hours played per week couldn't predict either accuracy (*F*(1, 56) =0.01, *p*=.89, *η*<0.001), or reaction times (*F*(1, 56) =0.0002, *p*=.98, *η*<0.001) on the MR task across conditions.

### *2.4.3 Testosterone results*

One woman was excluded from this analysis due to abnormal free testosterone levels (more than three standard deviations away from the mean). On average, men showed higher mean levels of free testosterone compared to women, as well as a lower digit ratio (see table 2). Salivary testosterone showed no significant relationship with accuracy, nor with reaction times. When inserted in linear models separately for men and women, it failed to show a significant effect in predicting performance either for accuracy (respectively $F(1,27)=0.72$, $p=0.72$, $\eta<0.001$; $F(1,26)=0.61$, $p=0.44$, $\eta=0.02$) or reaction times (respectively $F(1,27)=1.16$, $p=0.18$, $\eta=0.04$; $F(1,26)=0.06$, $p=0.79$, $\eta= <.001$).

Similarly, digit ratio showed no significant relationship to accuracy or to reaction times. When inserted in linear models separately for men and women, it failed as well to show a significant effect in predicting performance either for accuracy (respectively $F(1,20)=0.06$, $p=0.79$, $\eta<0.001$; $F(1,26)=0.61$, $p=0.42$, $\eta=0.03$) or reaction times (respectively $F(1,20)=1.09$, $p=0.3$, $\eta=0.05$; $F(1,19)=0.72$, $p=0.4$, $\eta=.04$).

Quadratic regressions to check for a potential U-shaped link between performance (accuracy and reaction time) and salivary testosterone also failed to produce significant results.

**Table 2.** Mean testosterone levels (salivary on left, prenatal on right) for both men and women.

| | **Salivary testosterone** | **Digit ratio** |
|---|---|---|
| | Mean +- SD | Mean +- SD |
| Men | 286 +- 111 | 0.97 +- 0.03 |
| Women | 61.1 +- 27.9 | - 0.04 |

## 2.5 Discussion

The aim of this study was to investigate gender differences in an MR task where either a motor strategy, a visuo-spatial strategy, or no specific strategy was imposed. In addition, we aimed to develop and test a new tool for studying MR in three dimensions, with the aim of transferring the design to a future fMRI study. Our results contribute to the existing literature by highlighting the influence of strategy on MR performance across sexes and provide a basis for future neuroimaging studies.

Consistent with previous research, our results showed that men outperformed women on MR tasks, exhibiting higher accuracy across all conditions, with significant differences observed in the control and object-based conditions. This finding is consistent with numerous studies that have consistently reported superior MR performance in men (Halpern, 2013; Linn & Petersen, 1985; Voyer et al., 1995). The object-based condition, which relies on spatial transformations using the object as a reference frame, showed a greater advantage for men, supporting the hypothesis that men may spontaneously adopt more efficient spatial strategies (R. Shepard & Metzler, 1971).

Regarding reaction times (RTs), we did not observe any difference between men and women. However, this result was expected due to the fact that the task design did not allow for RTs to track the MR process, as the MR was already completed when the target image appeared.

Interestingly, the effector-based condition showed a different pattern, where the difference in accuracy between the sexes did not reach significance. Within women, there was a notable increase in accuracy when using the effector-based strategy compared to the control condition, suggesting that this strategy may be particularly advantageous for women, possibly due to differences in spatial cognitive processing. Some studies have used the same hypothesis to explain gender differences in other areas of spatial ability. For example, in a navigation task, researchers have shown that women rely more on external landmarks in spatial tasks, whereas men rely more on spatial updating through self-motion (Lambrey & Berthoz, 2007). Similarly, Ferguson and colleagues (2019) showed that when faced the virtual Morris water maze, women showed a stronger preference for effector-based navigation than men, but both sexes could use both object-based and effector-based strategies. This supports the notion that cognitive strategies can be tailored to optimize performance between sexes.

On the other hand, it seems that forcing men to use different strategies doesn't seem to affect their performance. The reason for this stability could be that men maintain their own frame of reference even when confronted with an alternative approach, because it is the most effective one. A 2015 study (Boone & Hegarty) came to the same conclusion when using the Mental Rotations Test (Vandenberg & Kuse, 1978). Two experiments tested the theory that men are more aware of structural differences than women are, and that the gender gap can be explained by a strategy that exploit these differences. However, imposing different strategies on men didn't affect their performance advantage over women in mental rotation tasks. Alternatively, the stability for male performance may be due to their superior spatial ability (for a systematic review see Yuan et al., 2019), which would allow them to adapt remarkably well to the imposition of alternative strategies.

Regarding RTs, we observed a significant effect of condition, with RTs in the control condition being longer on average than in the other two experimental conditions. This can be explained by the fact that the control condition was always performed first. Thus, the longer reaction times were probably due to the novelty of the exercise.

Our analysis also revealed significant interactions between condition and block, even though post-hoc tests didn't reveal any significant effect, there seems to be a learning effect across the blocks. In particular, the control condition showed a general improvement in accuracy over time, suggesting a learning or familiarization effect with the task (Figure 5). Similarly, we can see that the reaction times decrease over the blocks and to then stabilize (see Figure 6). This suggests to believe that the control condition served as a training for the subsequent experimental conditions. For this reason, and contrary to our expectations, we were not able to compare the performance of the control condition with that of an experimental condition, which would have reflected the strategy spontaneously adopted by our participants.

Contrary to our expectations, no significant effects of video game experience on MR performance were found. This finding contradicts previous studies suggesting that video game training can improve spatial abilities and reduce gender differences in MR tasks (Feng et al., 2007; Nazareth et al., 2013). The discrepancy might be due to the specific sample or methodology used in our study. Similarly, no significant relationships were observed between salivary testosterone levels, digit ratio, and MR performance. These findings are in line with some previous studies that failed to find a consistent relationship between hormonal measures and MR performance (Gordon & Lee, 1993; Puts et al., 2010). However, it is important to note that the lack of effect here may also be due to the fact that the D2:D4 digit ratio is simply not an appropriate proxy for prenatal testosterone levels, as warned in the meta-analysis by Sorokowski & Kowal (2024).

Our study highlights the importance of considering strategy use in understanding gender differences in MR tasks. The differential impact of object-based and effector-based strategies on performance suggests that cognitive strategies play a critical role in MR abilities. Future studies should further investigate the neural correlates of these strategies using neuroimaging techniques, such as fMRI, to provide a more complete understanding of the underlying mechanisms. In addition, the serial presentation design used in this study appears to be effective in isolating the MR process. This design can be used in future neuroimaging studies to investigate the functional brain networks involved in MR without the interference of extraneous cognitive processes.

## 2.6 Limitations

One focus of our research has been how testosterone levels affect MR performance. But it's important to consider how women's sex hormones, such as progesterone and estradiol, also affect mental abilities. The strategies used for spatial tasks and MR performance can both be strongly influenced by changes in these hormones throughout the menstrual cycle (Bernal et al., 2020; Bernal & Paolieri, 2022; Scheuringer & Pletzer, 2017). According to Gurvich and colleagues (2023), women's performance on spatial tasks may vary depending on the phase of their menstrual cycle. Some studies suggest that women perform better during the follicular phase, when their estrogen levels are higher. For our study, we collected information about the participants' use of hormonal contraceptives for our study. One drawback of the current study is that we did not include this variable in our analysis. This aspect should taken into account in future studies to gain a better understanding of how testosterone interacts with sex hormones to affect MR performance.

Although the order of the experimental conditions (effector-based and object-based) was counterbalanced across participants, all participants began the test session with the control condition, which may have introduced order or learning effects that were not fully accounted for in the analyses.

## 2.7 Conclusion

In conclusion, our study confirms the robust gender differences in MR performance and highlights the influence of cognitive strategies on these differences. These results help to fill the gap in the field of gender differences and lead us to believe that men and women have a preferred strategy when performing a MR task. The serial presentation design offers a promising approach for isolating MR processes, paving the way for future neuroimaging investigations of the neural underpinnings of MR and gender differences.

# Chapter 3

## Experiment 2:

## Mental rotation-related neural interactions between gender and cognitive strategy

Manuscript published in Imaging Neuroscience, in September 2024. 10.1162/imag_a_00310. All the materials related to this paper (stimuli, data, and code for data analysis) are publicly available at the following GitHub repository: https://github.com/nadiaBRS/Mental-rotation-related-neural-interactions-between-gender-and-cognitive-strategy.

### 3.1 Abstract

A long-standing history of research has focused on the differences between men and women in cognitive tasks, including that men would be more accurate and faster than women in mental rotation (MR). This advantage suggests that men would use of an object-based cognitive strategy (OBS) to perform MR, whereas women would rely more on an effector-based cognitive strategy (EBS). To test this hypothesis, participants in the present study performed MR using OBS and EBS (plus a control condition) while their brain activity was recorded using fMRI. As sex hormones have often been reported to influence spatial ability, we also assessed the relationship between MR and testosterone levels and digit ratio. Behavioral results showed that (1) men performed faster MR than women in the OBS and control conditions, (2) men were more accurate than women in the OBS condition, and (3) women performed better in OBS than the other two conditions. No relationship was found between MR and testosterone or digit ratio. fMRI

data showed that women in the OBS condition had greater activation than men in the inferior frontal and somatosensory cortices. Salivary testosterone levels had no effect on whole-brain activity. Combining behavioral and brain imaging data, these findings suggest that the additional somatosensory activation found in women during OBS somehow affects their MR, preventing the use of a purely spatial strategy and promoting the use of body-based sensorimotor processing, which would result in lower accuracy. These results support that gender differences in MR would be better explained by considering their relationship with the cognitive strategies used to perform MR.

## 3.2 Introduction

The role of gender in cognitive differences has attracted great interest for long time, particularly with regards to spatial cognition. In this domain, mental rotation (MR) has often been found as easier/faster in men than women (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971; Voyer et al., 1995; Zapf et al., 2015). MR involves mentally rotating an object to understand its appearance after rotation without changing one's viewpoint. Rather than being fixed, MR is sensitive to several variables, including both experimental factors such as the stimuli's nature (Zeugin et al., 2020), point of view (Giovaola et al., 2022), and sensory modality (Pamplona et al., 2022), as well as contextual factors such as social interaction (Martinez et al., 2022). In this context, previous investigations on the potential influence of gender on MR have reported controversial results, indicating that gender might both primarily and secondary affect MR (Guizzo et al., 2019; Jost & Jansen, 2023; Sanchis-Segura et al., 2018). The origin of such a controversy has been associated with several hypotheses, including that men and women would rely on different cognitive strategies.

For instance, it appears that the many strategies that can be used to solve MR tasks (e.g. mental rotation, perspective taking, counting cubes, local turns, and global shapes) vary in their reliance on holistic versus piecemeal processing (Hegarty, 2018) and that men would spontaneously use a holistic approach while women would prefer a piecemeal approach (Boone & Hegarty, 2017).

In particular, it has been proposed that MR can be accomplished by using an object-based strategy (OBS, taking the object itself as a reference frame) or an effector-based strategy (EBS, taking the viewer's perspective as a reference frame) (Ionta et al., 2010;

Zacks & Michelon, 2005). The use of OBS or EBS results in different psychometric patterns. Specifically, the Response Time (RT) for MR in OBS correlates with the orientation of the target image, regardless any reference to the body of the participant. Conversely, in EBS the RTs for MR are affected by the participant's body constraints in that, for instance, in EBS the mental rotations oriented away from the midsagittal body plane (lateral rotations) take longer than rotations towards the midsagittal body plane (medial rotations) (Funk & Brugger, 2008; Pamplona et al., 2022). Since OBS has been associated with better accuracy and faster RTs (Halpern, 2013; Linn & Petersen, 1985; R. Shepard & Metzler, 1971) and men tend to show better performance when executing MR, it can be hypothesized that men spontaneously use OBS. Conversely, since women's MR is slower and EBS is slower and more prone to errors, it might be the case that women spontaneously use EBS. Nevertheless, beyond spontaneous choices, MR strategies can be voluntarily adopted. For example, OBS can be imposed by telling participants: "Imagine that the image is rotated on itself until it lines up with the other one" (Jordan et al., 2002; Wolbers, 2003). On the other hand, EBS can be imposed by a command such as: "Imagine that you turn the left image with your hand until it matches the right image" (Wolbers, 2003; Wraga et al., 2010).

Neuropsychological and imaging studies provided the necessary information about the neural correlates of MR. In particular, a meta-analysis (Tomasino & Gremese, 2016) found that, in addition to precentral and insular activations in the left hemisphere, MR bilaterally activates the inferior and superior parietal lobule, inferior frontal gyrus, middle frontal gyrus, supplementary motor area, inferior and middle occipital gyrus bilaterally, and cerebellum. In association with OBS, predominant activations are observed in occipital areas, as well as in right temporal and parietal regions. On top of the regions activated by OBS, EBS seems to activate mainly left sensorimotor regions.

Previous brain imaging studies reported very variable gender-related brain activations during MR. For instance, the inferior frontal cortex has been frequently associated with MR, but its activation has been reported as stronger in men than women (Mendrek et al., 2011), stronger in women than men (Hugdahl et al., 2006; Jiménez et al., 2010; Seurinck et al., 2004; Thomsen, Hugdahl, Ersland, Barndon, Lundervold, Smievoll, Roscher, et al., 2000; Weiss et al., 2003), as well as equally (Semrud-Clikeman et al., 2012) and differently (Christova et al., 2008) strong in women and men. Similarly, the parietal cortex is considered one of the brain regions mainly activated by MR, but its activation has been found only in men (Hugdahl et al., 2006; Thomsen, Hugdahl, Ersland, Barndon, Lundervold, Smievoll, Roscher, et al., 2000; Weiss et al., 2003), only in women (Jordan et al., 2002), and both in women and men (Semrud-Clikeman et al., 2012). Finally, the middle frontal cortex has been found as equally (Semrud-Clikeman et al., 2012) and differently (Christova et al., 2008) activated by MR in women and men. Altogether, previous findings do not allow to draw definitive conclusions about the impact of gender on the brain activity patterns associated with MR.

Variability in genetics and hormone exposure that affects spatial aptitudes may also play a role in gender-related differences in MR. It is known that in rats, testicular hormones influence spatial abilities during the perinatal period. For instance, in male rats the maze learning is adversely affected by neonatal castration (Dawson et al., 1975; Isgor & Sengelaub, 2003; Joseph et al., 1978; Williams et al., 1990), while in females the maze performance is improved by neonatal testosterone therapy (Dawson et al., 1975; Isgor & Sengelaub, 1998; Joseph et al., 1978; Roof & Havens, 1992; Stewart et al., 1975). Similar interplays between hormones and spatial abilities have been observed in humans too (Puts et al., 2007). This notion is supported by the links between spatial skills and congenital adrenal hyperplasia. In this syndrome, an enzyme deficit diverts cortisol precursors to the androgen pathway, resulting in excessive production of adrenal androgens (Pang et al., 1980). While masculinized spatial abilities have been suggested in affected females (Hampson et al., 1998; Hines et al., 2003; Resnick et al., 1986), contrasting findings have also emerged (Helleday et al., 1994; Malouf et al., 2006; McGuire et al., 1975). For instance, some studies reported poorer spatial ability in congenital adrenal hyperplasia males compared to healthy participants (Hampson et al., 1998; Hines et al., 2003), while others failed to report any significant differences (McGuire et al., 1975; Resnick et al., 1986). Another strand of literature suggests that the relationship between circulating testosterone and spatial abilities might not be linear, and would rather follow an inverted U-shaped curve, especially in men (Courvoisier et al., 2013; Moffat & Hampson, 1996; O'Connor et al., 2001). This model suggests that both low and high levels of testosterone could impair spatial cognition, while moderate levels might enhance it. The observed inverted U-shaped association may account for the observed discrepancy in findings across research on testosterone and spatial skills.

Investigations into potential links between early androgens and human spatial prowess have also sparked interest in digit ratio research. It has been suggested that the ratio of the second to fourth finger lengths (2D:4D) serves as a predictor of early androgen exposure, with men exhibiting a lower 2D:4D ratio compared to women (Manning et al., 1998). The sexual dimorphism in 2D:4D is believed to be impacted by prenatal sex hormones because of its early appearance. Numerous studies have therefore employed this anatomical marker to explore the potential impact of early androgens on spatial ability (Alexander, 2005; Austin et al., 2002; Coolican & Peters, 2003; Csatho et al., 2005; Kempel, Burk, et al., 2005; Kempel, Gohlke, et al., 2005; Loehlin et al., 2005; Manning & Taylor, 2001; McFadden & Shubel, 2003; Poulin et al., 2004; Putz et al., 2004). There is considerable variability in these outcomes, with some studies revealing positive associations, others uncovering negative correlations, and yet others detecting no significant connection, even within a single gender (review in Putz et al., 2004). Moreover, recent comprehensive research advises caution in interpreting digit ratios as proxies for testosterone levels. A meta-analysis by Sorokowski and Kowal (2024), which included data from 8077 participants, found no significant relationship between testosterone and the right or left 2D:4D, male or female 2D:4D, or between 2D:4D and testosterone measured in blood or saliva.

In the present study, we investigated the relationship between gender differences in MR-related performance (RTs and accuracy), cognitive strategy (limited to the comparison between OBS and EBS), and brain activity (fMRI), using an event-related design in fMRI. Our goal was to fill in the gaps in the field of gender differences in mental rotation by studying how men and women go about solving a MR task at the functional level, and how these activations vary according to the strategy used to solve the exercise. Thus, the aim of this study was to understand whether the use of a specific strategy could be at the root of gender differences in this domain. Furthermore, we tested whether different hormonal levels of testosterone were differentially associated with preferred strategies. We predicted that men would outperform women in the control and object-based conditions, whereas women's performance would be affected by the triggered strategy. We also predicted that women would show more brain activity than men in sensorimotor regions

## 3.3 Methods

### *3.3.1 Participants*

Since education can influence MR (Moè et al., 2021), we uniformed our sample to only university students. Thus 65 participants were recruited via a local online platform. Two participants were excluded due to an interruption of the experiment, and one participant was excluded to do excessive head motion in the MRI scanner. This yielded a final sample of 63 participants (33 females, age 25.33±3.8 y.o., range 19-33; 30 males, age 26.2±4.45, range 20-35). Based on effect sizes from preliminary experiment 1, we determined that our sample size would provide sufficient power for detecting moderate effects. Before entering the scanner, participants completed general health and fMRI compatibility questionnaires. Given the potential differences between perceived gender and biological sex (Wierenga et al., 2024), prior to the experiment all participants reported their perceived gender using a self-reported questionnaire. The questionnaire indicated that all participants had an alignment between perceived gender identity and biological sex. All participants were classified as right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Any type of neurologic or psychiatric disorder, claustrophobia, any kind of ferromagnetic implant, and left-handedness would have been considered an exclusion criterion for participation. Each participant gave written consent prior to their participation. The study was carried out in accordance with the 2013 Declaration of Helsinki criteria, with approval from the Friuli Venezia Giulia Regional Ethics Committee.

### *3.3.2 Procedure*

Based on a previous behavioral study (Bersier et al., in review), in the present event-related fMRI experiment participants were shown 60 pairs of 3D images. The two images of each pair corresponded to two out of the five images that were taken from the dataset developed by Shepard and Metzler (1971). For each pair, the first image represented a 3D image rotated with respect to the vertical and was presented for 1 s tailed by a blank screen of a jittered duration (from 1 to 3 s). Based on the data recorded during a pilot phase of the study, all the images had an intuitive vertical, defined mainly by the longer arms of the image. During the pilot we asked about 40 people to evaluate the verticality of thirty Shepard & Metzler figures. Then, only the images that were rated as vertical by the majority of the evaluators we selected for the experiment. A total of 10 rotation angles were possible, ±30°, ±60°, ±90°, ±120° and ±150°. Then, a cue appeared for 500 ms, representing either a circular arrow, a human hand, or a horizontal arrow and followed by a blank screen of 4.5 seconds. Then, the second image, representing a vertical 3D figure, was shown for 3 s. When the second image turned off, participants pressed one or another button to indicate whether the figure presented in the second image was congruent with the previously given instructions. To answer, participants had to press buttons on a keyboard placed on their chest. The trial ended with a jittered inter trial duration (6 s – duration of jitter 1), allowing all trials to have the same length of 15 seconds. The pairs of images were presented in two blocks of 30 trials. Between the blocks, a short break allowed participants to rest. The set of 60 pairs was selected randomly from the larger set, with the restriction that all five images and 10 rotation angles would be presented for each of them. All images were presented using PsychoPy (psychophysics software in Python (Peirce et al., 2019) ) and delivered through MRI-compatible goggles attached to the head coil.

### *3.3.3 Conditions*

In the control condition (Figure 1), the cue consisted of circular arrows, showing the direction of the rotation to be made (clockwise or counterclockwise in the picture-plane). The instructions were the following: "Look at the first image, then the cue. Mentally rotate the first image in the direction indicated by the cue, until the image is in its vertical position. Then compare the second image appearing on the screen with the result of your mental rotation, and indicate whether it is the same or different."

In the EBS condition (Figure 2), the cue was replaced by a human right hand, pointing left or right. Participants were instructed to imagine positioning their own hand as shown by the cue, grasping the 3D image shown at first, and mentally turning it in the picture-plane to its vertical position following the natural movement of the hand. Thus, if the hand cue pointed to the left, the movement to be imagined was clockwise, and if the hand pointed to the right, the imaged movement was counterclockwise. The explicit request to image using the right hand was intended to trigger an EBS and to use a reference frame the viewer's perspective.

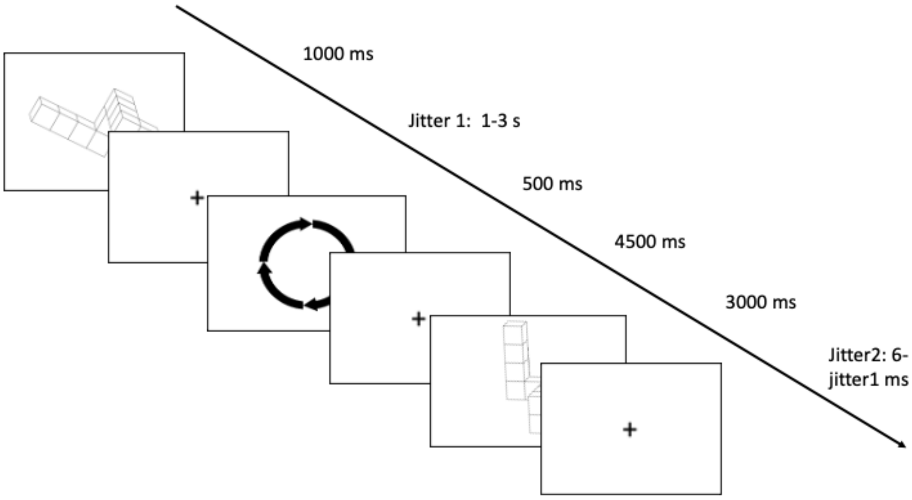

**Figure 1 – Example trial in the control condition.** In this condition, subjects were asked to mentally rotate the first image in the picture-plane, in the direction given by the arrows until reaching the vertical position. When presented with the second image, participants had to answer if it was congruent or incongruent with the instruction given. In the example, the trial is congruent.

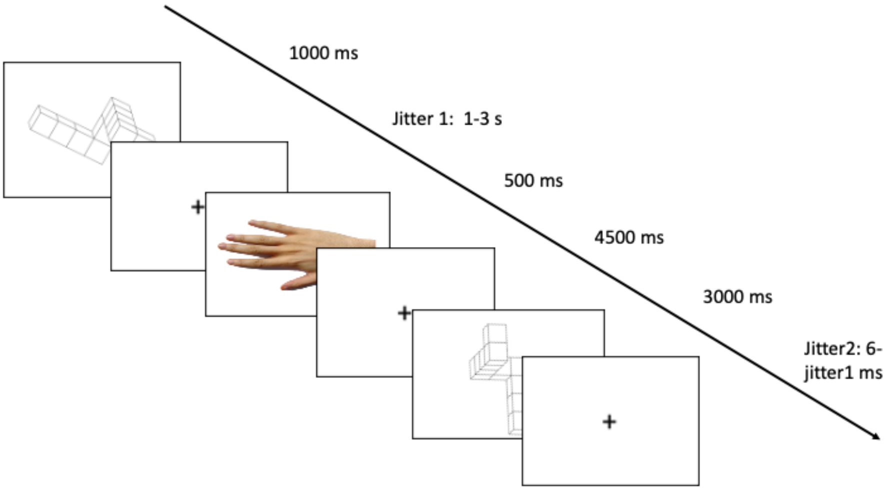

**Figure 2 – Example trial in the effector-based condition**. Subjects were asked to mentally rotate the first image in the direction given by the hand in the picture-plane, until reaching the vertical position, following the natural movement of a human right hand. When presented with the second image, participants had to answer if it was

congruent or incongruent with the instruction given. In the example, the trial is incongruent.

In the OBS condition (Figure 3), the first image had a red mark on one of its sides. The cue was a horizontal arrow, pointing either left or right. Participants had to mentally rotate the image in the picture-plane until it reached the vertical, so that the red mark would be on the side indicated by the arrow. In this condition, the cue was no longer indicating the direction of rotation, but the side where the mark should be in the final position. On the second image, the red mark was not shown. The red mark was intended to trigger a spatial (object-based) strategy, thus forcing the frame of reference to be the object itself.

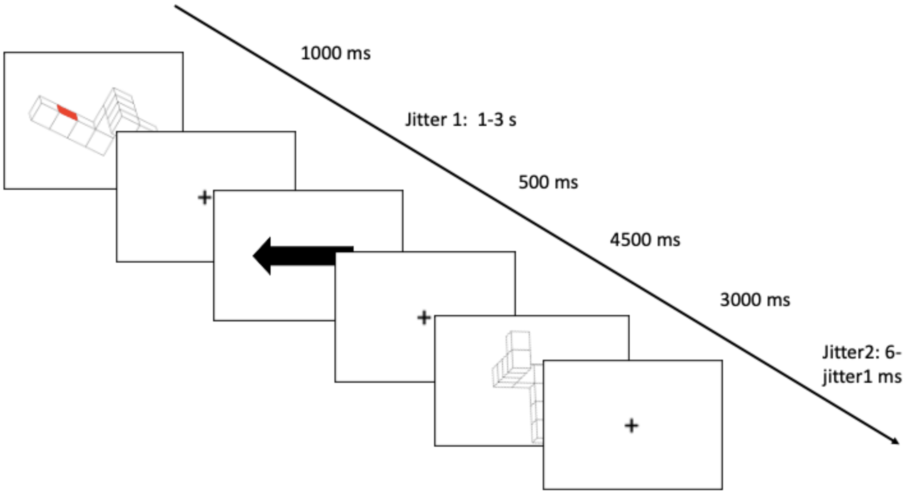

**Figure 3 – Example trial in the object-based condition**. Subjects were asked to mentally rotate the first image in the picture-plane, and in such a way that the red mark would end up on the side indicated by the direction of the arrow. When presented with the second image, participants had to answer if it was congruent or incongruent with the instruction given. In the example, the trial is incongruent.

In 50% of the cases, the answer was "congruent" (like in Figure 1), and in 50% of the cases, the answer was "incongruent". To add some difficulty, the "incongruent" answers were divided into two categories: "mirrored" (like in Figure 2) or "wrong rotation" (like in Figure 3), to avoid memorization of the mirrored images. All participants started the experiment with the control condition. Then, to account for the effect of the order of condition presentation, two orders were possible: order A in which the effector-based condition was presented before the object-based condition, and order B in which the object-based condition was presented before the effector-based condition. The experimental conditions were presented in a counterbalanced order. To familiarize with the task, for all three conditions, participants underwent a training session of 12 trials outside the scanner.

### *3.3.4 Hormone measure*

Saliva was tested for free testosterone, which is a measure of the physiologically accessible portion of testosterone in the bloodstream (Rilling et al., 1996). Prior to entering the scanner, participants were requested to provide a sample, by salivating at least two milliliters into a plastic tube. Samples were then stored at -20 degrees, until transported to the analysis laboratory, where they were immediately analyzed. Testosterone levels were measured with an enzyme-linked immunosorbent assay (ELISA) protocol (manufactured by IBL International GmbH, Germany). The assay sensitivity was 29,8 pmol/. The average intra-assay coefficient of variation was 5.6% and inter-assay imprecision was 8.7%. Regarding prenatal testosterone, the fingertip to the middle of the basal crease on the hand's palm was used to measure the lengths of the second (index finger) and fourth (ring) fingers. These numbers are divided to get the 2D:4D ratio (Brown et al., 2002).

### *3.3.5 MRI acquisition*

The MRI acquisition and preprocessing used here closely followed the approach used in Arbula et al. (2021). For consistency, with the editor's permission we reproduce the text used to describe it here, noting differences as appropriate.

MRI data was collected using a 3 Tesla whole-body scanner (Achieva Philips) with an 8-channel head coil at the "S. Maria della Misericordia" hospital in Udine. For each of the six runs of the mental rotation task, we collected 231 functional image volumes comprising 37 continuous axial slices. These images were acquired using a T2*-weighted echo-planar sequence with the following parameters: repetition time (TR) of 2 seconds, echo time (TE) of 30 milliseconds, flip angle (FA) of 82 degrees, voxel size of 3 × 3 × 3 mm, and acquisition matrix of 80 × 80. At the beginning of the session, we acquired a high-resolution T1-weighted anatomical image consisting of 170 sagittal slices. The parameters for this image were as follows: TR/TE of 8.1/3.7 milliseconds, FA of 12 degrees, voxel size of 1 × 1 × 1 mm, and acquisition matrix of 240 × 240. To account for spatial distortion in the functional images, we acquired a pair of spin echo images with opposite phase encoding directions, matching the orientation of the functional scans. These spin echo images were obtained at the beginning of each condition, for a total of 3 sequences.

### *3.3.6 MRI Quality Assessment Process*

MRI data were converted using the Dcm2Bids program (https://github.com/cbedetti/Dcm2Bids) from DICOM format to the Brain Imaging Data Structure (BIDS; https://bids.neuroimaging.io/). The MRI Quality Control tool (MRIQC) ( (Esteban et al., 2017) was then used to assess the quality of the structural and functional data. Using the MRIQCeption tool (https://github.com/elizabethbeard/mriqception), a comparison was done between the acquired quality metrics and a set of metrics from the MRIQC online API (Esteban, Markiewicz, et al., 2019).

### *3.3.7 MRI preprocessing*

The fMRI data were preprocessed using fMRIPrep version 1.5.1rc2 ((Esteban, Markiewicz, et al., 2019);RRID:SCR_016216) a Nipype ((Gorgolewski et al., 2011) RRID:SCR_002502) based-tool. The T1-weighted (T1w) volumes underwent intensity non-uniformity correction (INU) using N4BiasFieldCorrection (Tustison et al., 2010) distributed with ANTs 2.3.3 ((Avants et al., 2008) RRID:SCR_004757) and used as T1w-reference throughout the workflow. They were then skull-stripped using antsBrainExtraction.sh v2.2.0, based on the OASIS template. Brain surfaces were reconstructed using recon-all from FreeSurfer v6.0.1 ((Dale et al., 1999) RRID:SCR_001847), and the brain mask obtained previously was further refined with a customized approach reconciling ANTs-derived and FreeSurfer-derived segmentations of the cortical gray matter from Mindboggle ((Klein et al., 2017);RRID:SCR_002438). To achieve spatial normalization, the data were registered to the ICBM 152 Nonlinear

Asymmetrical template version 2009c ((Fonov et al., 2009);RRID:SCR_008796) using the antsRegistration tool of ANTs v2.2.0 ((Avants et al., 2008);RRID:SCR_004757). This registration involved brain-extracted versions of both the T1w volume and the template. Subsequently, brain tissue segmentation for cerebrospinal fluid (CSF), white matter (WM), and gray matter (GM) was performed on the brain-extracted T1w data using fast (FSL v5.0.9);((Y. Zhang et al., 2001);RRID:SCR_002823). The functional data underwent slice time correction using 3dTshift from AFNI v16.2.07 ((Cox, 1996);RRID:SCR_005927) and motion correction using mcflirt (FSL v5.0.9) (Jenkinson et al., 2002). Distortion correction was performed using an implementation of the TOPUP technique (Andersson et al., 2003) with 3dQwarp (AFNI v16.2.07);(Cox, 1996). Co-registration to the corresponding T1w data was done using boundary-based registration (Greve & Fischl, 2009) with six degrees of freedom, employing bbregister (FreeSurfer v6.0.1). The transformations for motion correction, field distortion correction warp, BOLD-to-T1w transformation, and T1w-to-template (MNI) warp were combined and applied in a single step using antsApplyTransforms (ANTs v2.2.0) with Lanczos interpolation.

To handle physiological noise, CompCor (Behzadi et al., 2007) was used to extract principal components for the anatomical CompCor variants (aCompCor). A mask excluding cortical signal was created by eroding the brain mask, leaving only subcortical structures. Six aCompCor components were calculated within the intersection of the subcortical mask and the union of CSF and WM masks derived from the T1w data, projected to the native space of each functional run. Frame-wise displacement (FD) and DVARS (Power et al., 2014) were calculated for each functional run using the Nipype implementations.

Further processing involved masking the functional data using the brain mask obtained from fMRIPrep. Fourteen fMRIPrep-derived confounds (six motion parameters, FD, standardized DVARS, and six aCompCor components) were removed at a voxel-wise level using the Denoiser tool (Tustison et al., 2010). Finally, the functional data were spatially smoothed using a Gaussian kernel with a full-width at half-maximum of 6 mm.

### *3.3.8 Behavioral data analysis*

We collected accuracy and RTs data. RTs were filtered for errors and outliers above 3 standard deviations from the group mean for each condition. Statistical analyses were performed with RStudio (https://rstudio.com/). Analyses of variance (ANOVA) were performed to explain the mean reaction time as well as accuracy, with gender, condition, testosterone, digit ratio as well as order of the task as factors. Our main hypotheses of gender differences in MR strategies were additionally tested by contrasting condition|gender and gender|condition (library 'emmeans') for the planned comparisons as specified in the Introduction section. If a significant effect was found for expected differences (such as differences in favor of males for accuracy and reaction time) paired comparisons Tukey-corrected for multiple comparisons were made.

Regarding testosterone and digit ratios, additional correlations were performed with both accuracy and reaction time. Since men have significantly higher levels of free testosterone than women, these analyses were carried out separately for the two groups.

### *3.3.9 fMRI data analyses*

#### First-level GLM analysis

For the first-level General Linear Model (GLM) analysis, FSL FEAT was used (www.fmrib.ox.ac.uk/fsl). A separate GLM model was constructed for each participant and each run, where the three experimental conditions (control, object-based and effector-based) served as the regressors of interest, and their temporal derivatives were included as regressors of no interest. The regressors were convolved with a double-gamma hemodynamic response function and timed with the presentation of the first image. The period of interest for the hemodynamic response analysis is described in the section Univariate analysis. We used FILM pre-whitening to adjust for autocorrelation, and a high-pass filter with a 100-second cutoff was used to remove low-frequency drifts.

#### Group-level GLM analysis

Using mixed effects (FLAME 1) as implemented in FSL, a whole-brain group-level analysis was carried out to determine mean group effects. A cluster-based method was used to threshold the statistical map, using a $Z > 2.3$ threshold. Family-wise error correction was then applied to make adjustments at $p = 0.05$.

## Univariate analysis

To study precisely the time windows during which the mental rotation was performed, we isolated the period of interest as the one following the cue, for a duration of 4.5 seconds. To explore the distinctive neural activations corresponding to each condition, six separate contrasts were performed. Additionally, we included group as a regressor to determine whether any observed effects were influenced by the gender.

## Testosterone analysis

Using within-group linear regression analysis, correlations between salivary testosterone and mental rotation-related brain activity were examined to look into a possible relationship with sex hormones. Testosterone levels were mean centered across all subjects and included as a regressor in the third level analysis' GLM model. The analysis was done for all individuals included in the same group, but given that men naturally have more testosterone than women, the analysis was spotted for both groups separately. The analysis was repeated for each experimental condition separately. Additionally, to investigate a potential non-linear relationship between free testosterone and performance (accuracy and reaction time), we ran quadratic regressions to verify that a possible U-shaped relationship did not exist.

In whole-brain and region-of-interest (ROI − described below) analyses, we investigated if correlations between brain activations and testosterone levels could be found. The ROI analysis minimizes the amount of voxel-wise multiple comparisons as compared to whole-brain mapping and may identify effects that would go unnoticed otherwise. We selected the difficult (150 degrees of rotation) and easy trials (30 degrees of rotation) to create a contrast representing the maximal cognitive effort. Runs were then averaged across conditions and beta-values for each subject extracted and correlated (Pearson correlation) to their respective salivary testosterone. Regions of interest (ROIs) for visuo-spatial strategy and motor strategy were chosen according to Tomasino & Gremese meta-analysis (Tomasino & Gremese, 2016). Regions specifically associated for visuo-spatial strategy were i) R Precuneus, ii) R Superior frontal gyrus, iii) R Superior occipital gyrus, iv) L Middle occipital gyrus, v) L Superior parietal lobe, vi) L Inferior temporal gyrus, vii) L Middle occipital gyrus, viii) R Posterior medial frontal gyrus. Regions specifically associated for motor strategy i) R Postcentral gyrus (Areas 2, 3b, 4p), ii) L Inferior parietal lobe, postcentral gyrus (Areas 2, 1, 3b), iii) L Superior parietal lobe, iv) R Angular gyrus. ROIS were created by designing five-mm-radius spheres centered in the coordinates. This procedure was done across all conditions, to check for differences in strategies.

## 3.4 Results

### *3.4.1 Behavioral results*

The analysis of variance revealed significant main effects of condition [F(2, 180) = 18.19, p<.001] and gender [F(1,180)=8.66, p=.003] on accuracy. Additionally, a significant interaction between the condition and the order of the tasks was found [F(2,180)=3.84, p=.023]. When looking at pairwise differences between gender within each condition, we found a significant difference among women between the OBS and control condition [t(1,180)=-3.04, p=.007], as well as between the OBS and EBS [t(1,180)=-2.68, p=.021]. When doing the same among men, the same significant differences were found, between OBS and control condition [t(1,180)=-4.78, p<.001], and OBS and EBS [t(1,180)= -4.64, p<.001] (Figure 4).

**Table 1.** Mean accuracy and reaction time (RT; seconds) for each condition across groups

| | **Accuracy Mean±SD** | | | **RT(s) Mean±SD** | | |
|---|---|---|---|---|---|---|
| **Condition** | control | OBS | EBS | control | OBS | EBS |
| **Men** | 0.68 ± 0.09 | 0.81 ± 0.14 | 0.68 ± 0.06 | 1.14 ± 0.32 | 1.05 ± 0.31 | 1.08 ± 0.33 |
| **Women** | 0.65 ± 0.08 | 0.73 ± 0.13 | 0.66 ± 0.11 | 1.34 ± 0.36 | 1.27 ± 0.38 | 1.23 ± 0.41 |

When investigating the main effect of gender, the only significant difference was found in the OBS, where men outperformed females [*t*(1, 180) =-2.99, *p*=0.003] (Figure 4).

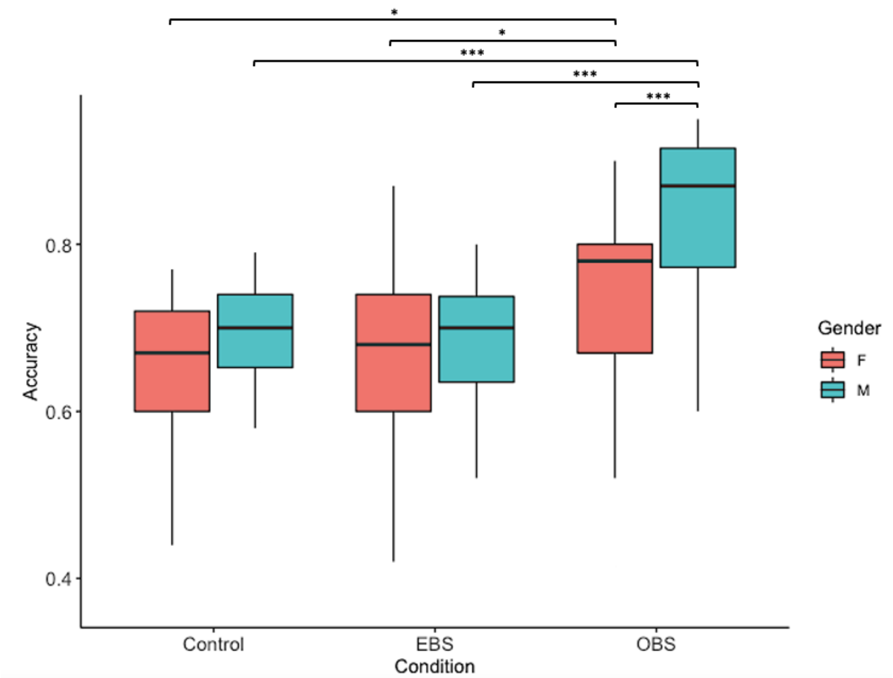

**Figure 4** – Accuracy across conditions and separated by gender. Paired comparisons with t-tests (corrected for Tukey) revealed significant differences within the OBS condition. For men, paired comparisons with t-tests (corrected for Tukey) revealed significant differences between the OBS and the EBS condition, as well as between the OBS and EBS conditions. Similarly for women, significant differences were found between the OBS and control conditions, as well as between OBS and EBS conditions. *Notes a significant different $p < 0.05$, ***Notes a significant difference $p < 0.001$.

Regarding the interaction between condition and the order of the tasks, a significant effect was found in the OBS condition [$t(1, 180)=3.29$, $p.=001$)], were scores were higher in the A order of the experiment (in which the effector-based condition was presented before the object-based condition) compared to B (Figure 5).

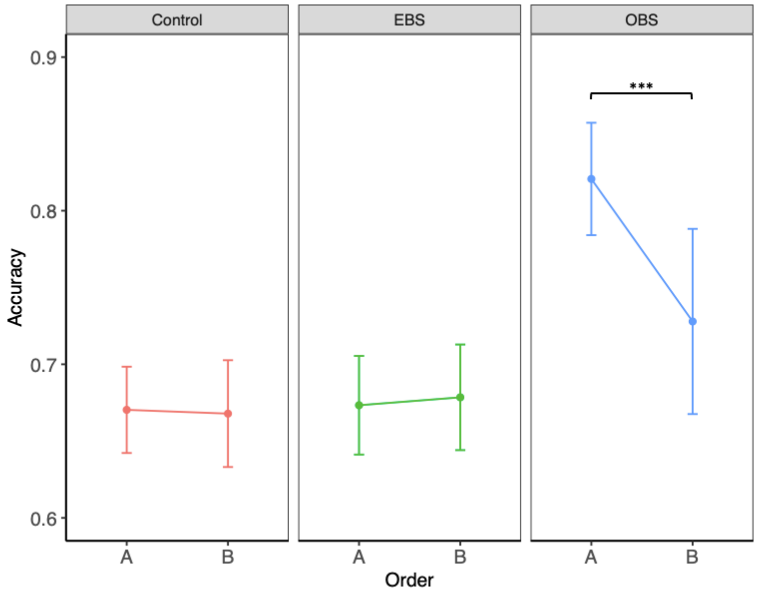

**Figure 5** – Accuracy across conditions and separated by order. T-tests corrected for multiple comparisons revealed a significant difference within the OBS condition were the scores for the A order were higher than B order, t(1, 180)=3.29, p=.001. ***Notes a significant difference p < 0.001.

As for reaction times, the analysis of variance revealed a significant effect of gender. Planned comparisons showed that men had shorter reaction time compared to women in the OBS [*t*(1,183) = 2.451, *p*=.0152], as well as in the control condition [*t*(1,183) = 2.234, *p*=.0267]. No gender difference was revealed within the EBS (Figure 6).

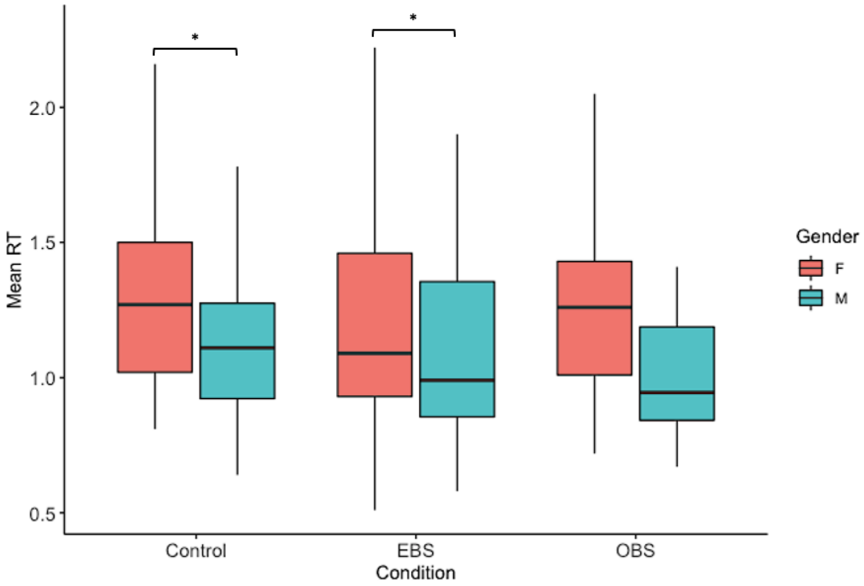

**Figure 6** – Mean reaction time for each condition separated by gender. Paired comparisons with t-tests (corrected for Tukey) revealed significant differences within the OBS condition and the control condition. *Notes a significant different $p < 0.05$.

### *3.4.2 Testosterone results*

The male group presented a mean free testosterone concentration of 257 pmol/L (SD=134), while the female group presented a mean concentration of 59.3 pmol/L (SD=35.3). For the digit ratio, men had a ratio of 0.97 (SD=0.04) between the second and fourth digit, while women had a ratio of 0.98 (SD=0.03). No link was found between measures of testosterone and behavioral data. Salivary testosterone as well as digit ratio showed no significant correlation with accuracy nor RT with the general MR score, or with any of the specific conditions (Table 2). When inserted as a factor in the analysis of variance, separately for men and women, no significant effect arose. Quadratic regressions to check for a potential U-shaped link between performance (accuracy and reaction time) and salivary testosterone also failed to produce significant results.

**Table 2.** Correlation (Pearson's *r*) table for testosterone measures and between group performance across conditions as well as for the mean MR accuracy and reaction times

| | **Men** | | | | **Women** | | | |
|---|---|---|---|---|---|---|---|---|
| | Free testosterone | | Digit Ratio | | Free testosterone | | Digit Ratio | |
| | r accuracy | r RT | r accuracy | r RT | r accuracy | r RT | r accuracy | r RT |
| **Mean** | 0.14 | -0.06 | -0.08 | -0.02 | 0.04 | 0.12 | -0.06 | -0.02 |
| **Control** | 0.15 | -0.07 | -0.001 | -0.07 | -0.08 | 0.13 | -0.13 | -0.07 |
| **OBS** | 0.11 | -0.04 | 0.02 | -0.02 | -0.21 | 0.28 | 0.02 | 0.16 |
| **EBS** | 0.16 | -0.06 | -0.18 | -0.03 | 0.27 | -0.09 | -0.11 | 0.01 |

### *3.4.3 Neuroimaging results*

**Whole brain**

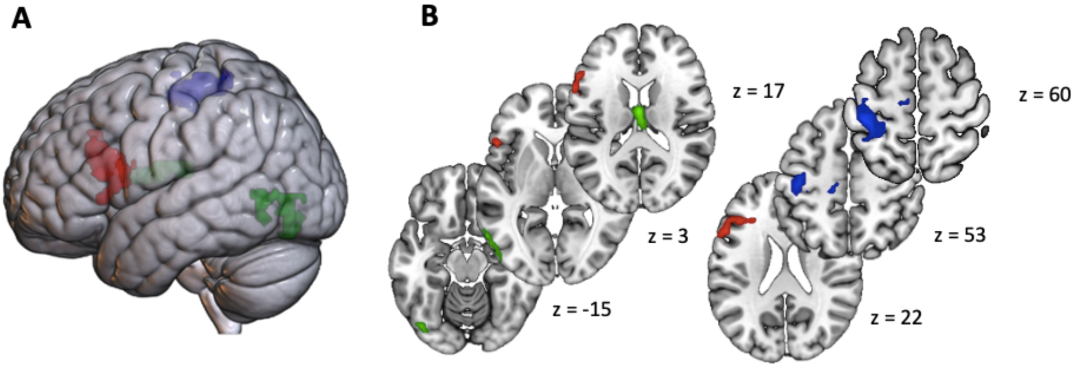

**Figure 7 –** Rendered 3D brain (A) and axial slices (B) showing significant contrast activations. Brain activations from the whole-brain voxel-wise OBS–control contrast are shown in red; brain activations from EBS–OBS contrast are shown in blue; brain activations from EBS–control are shown in green. The statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, corrected at $p = .05$ (family-wise error correction).

The OBS-control contrast at the group level showed a main cluster of activation in the left inferior frontal cortex, in the opercular and triangular sections (Figure 7, Table 3).

The EBS-OBS content contrast at the group level showed left activations in regions typically associated with motor and sensorimotor processing, comprising the supplementary motor cortex, as well as postcentral and precentral gyrus, the middle cingulum, and the superior parietal lobe (Figure 7, Table 3).

The EBS-control contrast at the group level showed two main clusters of activations. The first comprised the thalamus and caudate, bilaterally. The second comprised exclusively left areas and included the middle temporal, inferior and middle occipital cortex, as well as fusiform gyrus (Figure 7, Table 3).

Finally, when doing a two-sample t-test to study the effect of gender, a significant cluster arose in the F>M contrast. Areas where located in the right hemisphere and englobed the superior temporal lobe, the rolandi operculum, the supramarginal gyrus and the inferior frontal gyrus.

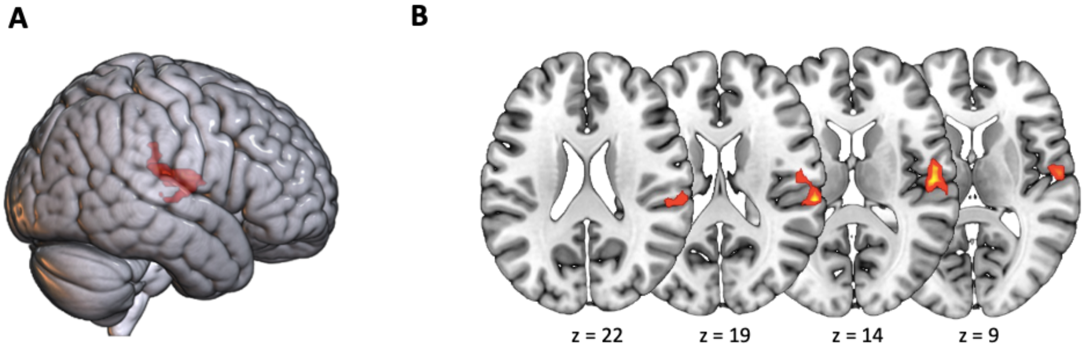

**Figure 8 –** Rendered 3D brain (A) and axial slices (B) showing significant OBS–control contrast activations with gender as a covariate. Brain activations from the whole-brain voxel-wise OBS–control contrast for F > M. The statistical map was assessed with a cluster-based threshold of $Z > 2.3$, corrected at $p = .05$ (family-wise error correction).

**Table 3**. Significant clusters from whole brain

| | MNI | | | Peak Z | Cluster level | |
|---|---|---|---|---|---|---|
| | x | y | z | | Size | p |
| **EFFECTOR-BASED vs. OBJECT-BASED** | | | | | | |
| L Postcentral Gyrus | -39.5 | -30.5 | 65.5 | 3.67 | 163 | 0.0005 |
| L Precentral Gyrus | -39.6 | -15.5 | 53.5 | 3.54 | | |
| L Mid Cingulum (BA6) | -12.5 | -24.5 | 50.5 | 3.42 | | |
| L Postcentral Gyrus | -27.5 | -39.5 | 59.5 | 3.26 | | |
| L Superior Parietal lobe | -33.5 | -45.5 | 65.5 | 3.13 | | |
| L Supplementary motor | -9.5 | -18.5 | 59.5 | 2.75 | | |
| **EFFECTOR-BASED vs.CONTROL** | | | | | | |
| L Thalamus | -0.5 | -9.5 | 17.5 | 4.45 | 89 | 0.002 |
| R Caudate | 8.5 | 5.5 | 11.5 | 2.99 | | |
| L Caudate | -6.5 | 2.5 | 11.5 | 2.87 | | |
| R Thalamus | 11.5 | -12.5 | 11.5 | 2.52 | | |
| L Middle Temporal | -60.5 | -63.5 | -0.5 | 4.54 | 85 | 0.029 |
| L Inferior occipital | -48.5 | -78.5 | -9.5 | 3.52 | | |
| L Fusiform gyrus | -42.5 | -78.5 | -15.5 | 3.37 | | |
| L Middle Temporal | -57.5 | -69.5 | 2.5 | 3.25 | | |
| L Inferior Temporal | -54.5 | -63.5 | -9.5 | 2.98 | | |
| L Middle occipital | -48.5 | -75.5 | -0.5 | 2.74 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| **OBJECT-BASED vs. CONTROL** | | | | | | |
| L Inferior frontal gyrus | - 57.5 | 23.5 | 14.5 | 3.5 | 164 | 0.0003 |
| L Inferior frontal gyrus | -48.5 | 26.5 | 29.5 | 3.46 | | |
| L Inferior frontal gyrus | -51 | 20.5 | 2.5 | 3.33 | | |
| L Inferior frontal gyrus | -36.5 | 26.5 | 32.5 | 3.26 | | |
| L Inferior frontal gyrus | -30.5 | 26.5 | 23.5 | 3.2 | | |
| L Inferior frontal gyrus | -57.5 | 11.5 | 8.5 | 3.13 | | |
| **F>M for OBJECT-BASED vs. CONTROL** | | | | | | |
| R Superior temporal | 62.5 | -27.5 | 20.5 | 3.81 | 110 | 0.006 |
| R Rolandic operculum | 53.5 | -15.5 | 14.5 | 3.79 | | |
| R Supramarginal gyrus | 50.5 | -27.5 | 32.5 | 3.47 | | |
| R Superior temporal | 62.5 | -21.5 | 17.5 | 3.17 | | |
| R Inferior frontal gyrus | 56.5 | 21.5 | 2.5 | 2.53 | | |

### *3.4.4 Testosterone results*

When included in the GLM as a regressor, levels of salivary testosterone showed no interaction with whole brain activation, for any of the experimental conditions. ROI analyses for the hard<easy contrast were conducted with the areas cited in section 2.7.4 and corrected for multiple comparisons. Individual beta-maps within the ROIS were correlated to the testosterone levels for each participant and each condition. Correlation tests didn't reveal any significant correlation between the activations within the ROIs and the individual salivary testosterone levels.

## 3.5 Discussion

The present study investigated how the brain activity related to MR is affected by cognitive strategy and gender. The results showed that (1) men's and women's behavioral performance was affected by the cognitive strategy used to solve the MR task (higher accuracy in the OBS condition for men than women), (2) imposing different strategies to perform MR activated different brain regions, and (3) gender differences were reflected in different brain activation patterns for MR.

### *3.5.1 Cognitive strategy and brain activity*

The OBS significantly activated the pars opercularis with respect to the control condition. Some studies have shown that this area is activated during spatial processing tasks, such as MR and space-related processing  tasks (Wiesen et al., 2022). In particular, the left pars opercularis has been found to be more active during mental rotation of objects and images (Tomasino & Gremese, 2016). In line with these findings, it seems that individuals successfully engage into a “spatial” strategy in comparison to the control condition. Moreover, the object-based condition showed greater accuracy for both males and females at the behavioral level, compared to the control condition. Thus, activation of the pars opercularis in OBS engagement is associated with greater overall accuracy and suggests that it is a key structure in explaining the spatial strategy efficiency.

In the EBS-OBS contrast, significant activation of the motor and sensorimotor cortices was observed. In EBS, participants were specifically guided to mentally reach, grasp and rotate the image using their right hand. The imagery results seem to reflect the use of a motor strategy, as well as embodiment processes, indicating that participant were successfully triggered into an effector-based perspective, with respect to the OBS condition. Interestingly, at the behavioral level, MR in OBS had greater accuracy than in EBS and control condition (see figure 4). The novelty here lies in the fact that we were able to link performance, strategy and brain activation, and thus provide a clue as to why motor strategy is commonly less effective than others. It is therefore possible that the additional activation of sensorimotor regions may compromise the efficiency of MR processes, resulting in poorer performance.

With respect to the control condition, EBS activated the thalamus. Although it is not the brain region the most prominently associated with MR, the thalamus has been involved in MR-related research (Butler et al., 2006; Calhoun et al., 2001; Potvin et al., 2013; Schweinsburg et al., 2012; Thérien et al., 2022). In addition to being a relay for most sensory information, this structure also has a key role in the body representation system, that encompasses the neuronal representations of the body and is therefore crucial for understanding how motor functions operate (Ehrsson et al., 2003; Longo & Haggard, 2010). In a series of studies, Naito et al. suggested that the thalamus is a component of the sensorimotor control network that helps with both online movement control and the development of body images (1999; 2002; 2016; 2006). Recently, it has also been shown that the thalamus plays an important role in vestibular processes (review in Wijesinghe et al., 2015). Therefore, the thalamic activation found in our contrast might be related to the self-oriented and vestibular processing induced using an effector-based strategy in that condition. Finally, EBS significantly activated the occipitotemporal cortex. This area is known to be involved in the visual-spatial processing of the rotated objects and plays a crucial role in the mental manipulation of visual information (Haxby et al., 2001). Hence, the observation of its activation in a context eliciting manual object manipulation is highly coherent.

### *3.5.2 Gender Differences*

Behavioral results on accuracy show that when imposed with an object-based strategy, performances increase, regardless of the gender (see figure 5, table 1). This goes in line with previous findings showing that using a spatial strategy to solve mental rotation is more effective (Halpern, 2013; Linn & Petersen, 1985; R. Shepard & Metzler, 1971). However, males still perform better than women in this condition. A possible explanation arises for this phenomenon when this behavioral result is linked with the functional data.

We found that gender affected the activity of specific brain regions. These findings are in line with previous electroencephalographic evidence that gender affects the temporal dynamics of the brain activity related to MR (Griksiene et al., 2019; Yu et al., 2009). When looking at the contrast OBS-control separated by gender, we observe that females activated an additional cluster in the somatosensory cortex (Figure 8). This area is known to play an important role in processing tactile and proprioceptive information related to the body and its movements. Studies suggest that during MR tasks, the somatosensory cortex is involved in the simulation of body movements and the generation of a kinesthetic image of the body in space (de Lange et al., 2006; Maravita & Iriki, 2004; Parsons, 1994; Perruchoud et al., 2016). This process involves the recruitment of the body schema, which is a representation of the body's posture and movements in space. The body schema is thought to be essential for MR because it enables individuals to simulate the movements of an imagined object or body part in space (Amorim et al., 2006). During MR tasks, the somatosensory cortex is more active in women compared to men, suggesting that women may rely more on body-based processing during mental rotation

(Hughes et al., 2012). When linked to the behavioral results, this led us to believe that this additional activation somehow affects the mental rotation process and interferes with the deployment of a pure spatial strategy. These findings hold particular significance due to the lack of discernible distinctions in the remaining conditions, whether pertaining to behavioral or functional aspects. It is noteworthy that the parity in performance between men and women in the alternate two conditions implies that gender-based variations in the mental rotation task likely stem, to some extent, from strategic factors. Consequently, the well-known gender disparities consistently identified within the domain might be diminished, as they would exclusively relate to scenarios wherein participants are compelled to adopt a visuo-spatial strategy.

### *3.5.3 Testosterone*

This is even more interesting when the results of testosterone analyses are added to the equation. Some studies link testosterone levels to mental rotation performance (Burke et al., 2016; Hooven et al., 2004; Manning & Fink, 2018; Sadr et al., 2020). For example, Manning (2018) reports a negative correlation between 2D:4D and male performance, but not female performance. Nevertheless, neither Austin et al. (2002), Bersier et al. (submitted), nor Coolican and Peters (2003) discovered any such association in either sex, even with large population samples. In our study, when added as factors in an ANOVA, salivary testosterone did not help explain the difference in performance between genders. Quadratic regressions did not produce significant results, nor were Pearson correlations found with accuracy or reaction time (see Table 2). Furthermore, Schöning et al. (2007) found no correlation between MR performance and hormonal data in men and women, but did observe region-specific correlations between testosterone and task-related activity in the left inferior parietal cortex. Interestingly, one of our regions of interest in our ROI analysis is very close to the region cited in Schöning and colleagues x=-44, y=-30, z= 40 vs. x=-48, y=-54, z=34 for Schöning et al., 2007). Despite this proximity, we did not find any significant relationship in our analysis. This discrepancy might be attributed to differences in methodology, sample size, or specific aspects of task design and participant characteristics. Our findings, along with those of Schöning et al. (2007), highlight the complexity of the relationship between testosterone, brain activity, and cognitive performance, suggesting that further research is needed to unravel these intricate dynamics.

No effect was found for digit ratio in either in the ANOVAs or in the Pearson correlations. However, it is important to note that the lack of effect here may also be due to the fact that the D2:D4 digit ratio is simply not an appropriate proxy for prenatal testosterone levels, as warned in the meta-analysis by Sorokowski & Kowal (2024).

### 3.5.4 *Order of administration*

A further finding lies in the training effect of the effector-based condition on the object-based condition. As shown in Figure 5, when participants perform the effector-based condition first (order A), their accuracy in the object-based condition that follows is significantly higher compared to the opposite order (order B). This can be interpreted as a facilitating effect due to the training through a motor strategy. Moreover, this enhancement in performance was present in men and women alike. Thus, the effects of motor strategy should not be ignored. Although it leads to lower performance in terms of accuracy in a mental rotation task, it seems to increase performance when it precedes the deployment of a spatial strategy. This accidental finding merits further investigation in future work.

### 3.5.5 *Differences with experiment 1*

Overall, performance declined in the MRI setting compared to the behavioral environment, likely due to factors such as sensory overload, restricted movement, and limited response time inherent to MRI scanning. Additionally, participants in Experiment 1 performed tasks while sitting, whereas in Experiment 2 they were lying down in the MRI scanner, a positional change that could further influence cognitive performance. Abou Khahil (2020) found that certain cognitive tasks are affected by postural conditions, with performance in some tasks being better when sitting compared to other positions. This may be especially relevant in tasks involving mental rotation, as posture could influence spatial and visual-motor engagement. In line with this, van Maanen et al. (2016) observed that the scanner environment tends to increase response times and, to a lesser extent, error rates, likely due to a combination of motor slowing and reduced attentional focus.

In Experiment 2, the time window during which participant have to give a response was reduced compared to Experiment 1, passing from 4000 ms to 3000 ms. Time constraints in the MRI may also disproportionately impact female participants, as Resnick (1993) reported that females show a greater performance drop under timed conditions, potentially due to different problem-solving strategies. In our study however, the drop in accuracy was more pronounced for male participants across most conditions, except in the OBS condition, where performance remained relatively stable. This suggests that the object-based strategy may be resilient to various environmental and positional challenges posed by the MRI setting, providing a more stable framework that mitigates environmental effects and supports consistent task engagement.

## 3.6 Limitations

One limitation of this study is that the control condition was systematically performed at first. The motivation of this choice was to observe which strategy would be spontaneously used by the participants, in the absence of other indications, or any possible bias due to learning during the experiment.

The present study was designed to assess specifically the effect of testosterone on the brain activity related to MR. However, MR can be influenced by many other factors, including women's sex hormones . The present study focused the role of testosterone in mental rotation. Nevertheless, additional variations of other sex hormones, such as estradiol and progesterone, may play important roles in mental rotation. Investigating this topic could be the focus of future studies, which could recruit female participants during, for instance, early and late follicular phases, when estradiol and progesterone levels are different. Similarly, participants using oral contraceptives could be recruited during the inactive pill phase. This approach would help to recruit a more homogeneous group of women in terms of hormonal profiles and could provide more precise insights into the influence of sex hormones on mental rotation tasks.

It could be argued that participants may have started to mentally rotate the image before the cue. However, we would reject this hypothesis based on two main reasons. First, during a training session prior to the fMRI experiment, participants were explained and learned that they had to simply look at the target, without other mental activities, until the cue was presented. Second, to correctly accomplish the task participants had to wait for the cue which would indicate the direction of MR, since the vertical could be reached by turning the image clockwise or counterclockwise. This direction was given by the cue and, if participants would begin MR before the cue, they may have faced the possibility of having to correct their mental process, which would cost a lot of mental energy and may have resulted in the activation of larger brain networks, which we did not detect.

## 3.7 Conclusion

The present study investigated the effects of cognitive strategy and gender on MR - related brain activity. Our findings provide valuable insights into how different strategies and gender-specific factors influence both behavioral performance and underlying neural mechanisms during the mental rotation task. Behavioral results showed that men had higher accuracy in OBS compared to women. This difference was further elucidated by our fMRI data, which revealed that females showed additional activation in the somatosensory cortex in the OBS-control contrast, suggesting a reliance on body-based processing that may interfere with the deployment of spatial strategies. This finding suggests that gender differences in MR tasks are likely strategic rather than inherent, as performance was similar between genders in other conditions.

Importantly, we effectively demonstrated that different strategies, such as OBS and EBS, activate distinct brain regions and that these activations are associated with performance outcomes. In OBS, the pars opercularis – a region associated with spatial processing and mental rotation – was significantly activated. This activation correlated with higher accuracy for both groups, suggesting that OBS is an efficient spatial strategy. Conversely, EBS was associated with the activation of sensorimotor regions, reflecting the use of a motor strategy. However, EBS also resulted in a general lower accuracy at the behavioral level, suggesting that additional activation in sensorimotor regions may compromise the efficiency of MR.

Testosterone levels did not correlate with MR performance, challenging the notion that testosterone influences gender differences in spatial tasks. Finally, the order of administration showed that performing EBS first improved subsequent OBS performance for both groups, indicating a potential training effect from motor strategy to spatial strategy.

# Chapter 4

# Experiment 3:

# Gender shapes the brain activity associated with mental rotation of different images

Manuscript submitted in Cortex. All the materials related to this paper (stimuli, data, and code for data analysis) are publicly available at the following GitHub repository: https://github.com/nadiaBRS/Gender-shapes-the-brain-activity-associated-with-mental-rotation-of-different-images

## 4.1 Abstract

Recent evidence challenges the typical notion that men outperform women in mental rotation (MR) tasks, possibly due to the use of experimental protocols that either used only two types of MR images or where gender was added post hoc as a factor. The present study investigated how the interaction between gender and stimulus type affects the brain activity related to MR tasks. fMRI data were recorded while participants performed MR of abstract objects, real objects, and bodily figures. With respect to women, men had stronger inferior frontal activations during MR of abstract objects, and in superior and medial frontal areas during MR of bodily figures. Compared to men, women showed stronger activation in the superior parietal lobe during MR of bodily figures with respect to abstract objects, and in the right inferior occipital cortex in the MR of real objects versus bodily figures. Finally, men showed a positive relationship between accuracy and brain activity in the right precuneus, while women showed a negative relationship between accuracy and brain activity in right motor and premotor areas. These results

show that brain activity during MR is modulated by the type of images, differently for women and men.

## 4.2 Introduction

Mental rotation (MR), the cognitive ability to mentally perform rotational spatial transformations of objects' images, has been the focus of research in cognitive psychology and neuroscience for decades. This ability not only is crucial for everyday tasks such as navigation and object manipulation, but it also serves as a foundational ability in fields such as science, technology, engineering and mathematics.

MR is sensitive to participant- and stimuli-related variables. Participant-related factors include age (Castilla et al., 2022), ethnicity (Assari, 2020) and social interaction (Martinez et al., 2022). Gender appears to play a crucial role in MR, with men generally outperforming women (Halpern, 2013; Linn & Petersen, 1985; Long et al., 2021; Shepard & Metzler, 1971; Voyer et al., 1995; Zapf et al., 2015). This pattern further depends on the employed cognitive strategy, in that specifically when a visuospatial cognitive strategy is used in MR, women show additional activity in the somatosensory cortex compared to men (Bersier et al., 2024). Stimulus-related variables include semantics (Zeugin et al., 2020), viewpoint (Giovaola et al., 2022), visibility (Rotach et al., 2024) and sensory modality (Pamplona et al., 2022). Accordingly, right hemisphere lesions impair MR for external objects, while left hemisphere lesions affect MR of hands (Tomasino et al., 2003). MR of hands involves unilateral fronto-parieto-occipital activations, whereas MR of abstract objects involves bilateral parietal and occipital activations (Kosslyn et al., 1998). MR of bodily images activates bilateral sensorimotor regions, while non-bodily images activate unilateral parieto-occipital regions (Aso et al., 2007; Tomasino et al., 2004). MR of hand images alone activates sensorimotor regions, but when attached to a body, they activate somatosensory and visual regions (Perruchoud et al., 2016).

Some studies have shown that the mental spatial processing of known and unknown objects is different. Vingerhoets and colleagues (2002) found differences in the treatment of human hands and tools during MR. While premotor activation was bilateral for MR of hands, it was unilateral for MR of tools. These results suggest that in MR of hands, participants imagined moving both hands, whereas in the MR of tools they imagined using their dominant (right) hand. Petit et al. (2006) showed that electroencephalographic activity is different for MR of abstract and real objects, concluding that when a real object is presented in a graspable orientation, semantically related motor programs are automatically activated. Therefore, the behavior automatically evoked by the type of image used in MR influences the location of associated cortical activity.

Numerous studies have examined gender-related differences in MR of different types of images. For example, in the MR of 3D abstract objects, Jordan and colleagues (2002) showed that women have stronger temporo-parietal activations, while men have stronger activity in both motor cortices and unilateral parietal and parieto-occipital regions. Based on the observation that MR of 3D cubes was associated with parietal activations in men, and frontal activations in women, Hugdahl and colleagues (2006) suggested that different genders are biased towards different cognitive strategies. While men would tend towards a coordinate processing approach, women would adopt a categorical processing approach. Seurinck, Vingerhoets and de Lange (2004) showed that gender differences were limited to MR of hands, with women activating more left ventral premotor areas and men more occipital regions. Based on pupil dilation as a measure of cognitive effort, Campbell et al. (2018) found that MR of cube figures were less cognitively taxing for men, while no differences where observed during rotation of human hands.

Furthermore, it has been proposed that gender differences in MR are an epiphenomenon of the employed experimental protocols, since they can be abolished when MR (i) is performed with specific stimuli (Fisher et al., 2018; Jansen-Osmann & Heil, 2007; Rahe et al., 2018), (ii) occurs in specific settings (Parsons et al., 2004), and (iii) is controlled for participants' characteristics (Tan et al., 2003). Interestingly, Jansen et al (2020) reported no gender differences in MR performance despite gender was associated with different brain activity~~.~~

In sum, previous psychophysical and brain imaging investigations on the role gender in MR-related brain activity and performance produced mixed results, making it difficult to draw definitive conclusions. The inconsistence of previous findings may be due to methodological choices, such as the use of only two types of images in MR, or the selection of "gender" as a factor only post-hoc. This choice risks to intrinsically limit the conclusions, which would be based on only two extremes of what, in fact, could be a continuum between images with progressively different levels of abstraction. Thus, an experimental protocol with more types of MR images, including both different types of objects and body-related images, would allow a better investigation of the potential role of ecological validity of MR images. Images of real objects that are more familiar and with a stronger affordance to be manipulated may engage different cognitive strategies compared to images of abstract objects. The implementation of bodily figures may allow to explore the influence of embodied cognition, a factor that could be overlooked if only abstract and non-interactive objects would be used. According to this view, we used MR images representing abstract objects, bodily figures, and real objects, and we investigated whether gender-specific effects that may depend on image type. This approach aims at advancing the field of MR by offering a more nuanced examination of how image properties modulate the cognitive and neural processes involved in MR, further modulated by gender.

## 4.3 Materials and methods

### *4.3.1 Participants*

Sixty participants (29 women), aged between 18 and 35 years, took part to the study. The datasets from 3 of them were excluded due to below chance performance in MR. The definitive sample comprised 58 participants (29 women, mean age 24.17, SD= 4.12, range 19-35, and 28 men, mean age 25.29, SD=4.25, range 20-35). Prior to the experiment, each participant gave written informed consent and completed a magnetic resonance safety questionnaire, as well as a self-declaration of their gender identity. Participants were unaware of the research questions until the end of the experiment. Exclusion criteria were: age outside the pre-determined range (18-35 years); visual impairment without the possibility of correction; any type of neurological or psychiatric disorder; claustrophobia; pregnancy; any type of ferromagnetic implant; left-handedness as evaluated by a score below than the cut-off of 60 on the Edinburgh Handedness Inventory (Oldfield, 1971). The experimental procedures were approved by the local ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki (2013).

### *4.3.2 Stimuli*

During fMRI data recording, participants performed MR of 3 different images: abstract objects, bodily figures, and real objects (Figure 1). The 3D abstract objects consisted of 6 images like the ones used by Shepard and Metzler (1971). The bodily figures were taken from a previous study (curtesy of Amorim et al., 2006) and represented a full human body in 3 biologically possible and 3 biologically impossible postures. The 6 images classified as real objects represented objects that could be grasped by one hand only (bike break, wrench, stapler, corkscrew, spray bottle, bottle opener). All images were digitally manipulated in order to assure symmetry, absence of writings, and same overall size.

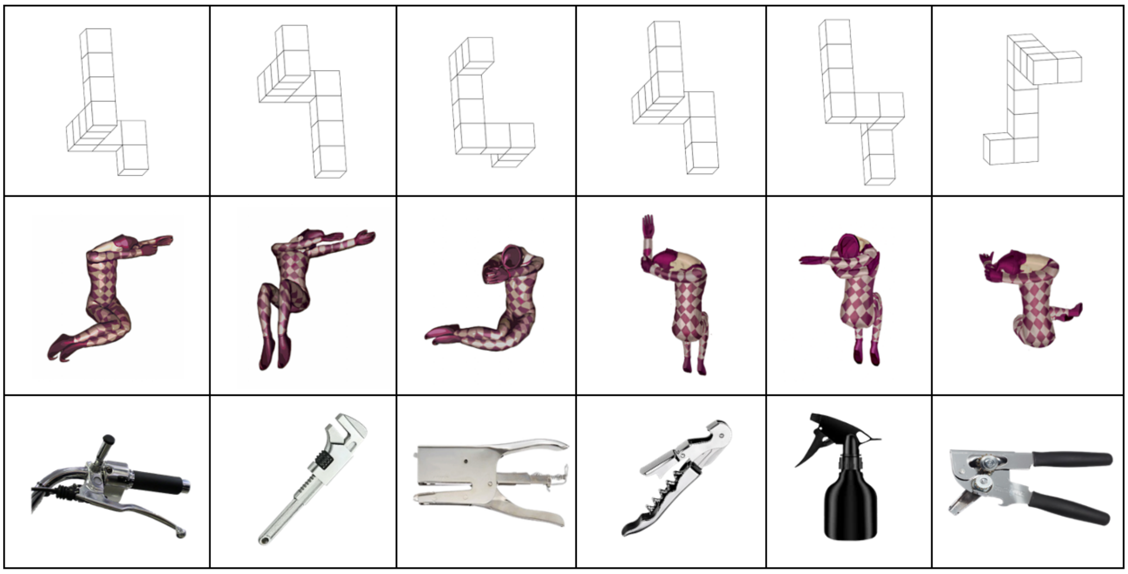

**Figure 1 – Experimental stimuli** consisted in images of abstract objects, bodily figures, and real objects.

### *4.3.3 Procedure*

During fMRI data recording participants performed a MR task according to the procedure described in (Bersier et al., 2024). Participants were shown 60 pairs of images. For each pair, the first image showed an item (abstract object, human body, real object) rotated by one out of 10 rotation angles (±30°, ±60°, ±90°, ±120° and ±150°) with respect to the vertical. This image was presented for 1500 ms, tailed by a blank screen of a jittered duration (from 500 ms to 1000 ms). Then, a cue appeared for 500 ms, representing a circular arrow turning in a clockwise or counterclockwise direction, followed by a screen displaying the word “GO” for 3500 ms. During this time, participants were asked to mentally rotate the first image until the vertical. They indicated when they completed this task by pressing a key, in order to collect their response time (RT). After the participant’s response, the “GO” screen remained visible with a jittered duration ranging from 500 ms to 1000 ms followed. Then, the second image of the pair was shown for 2500 ms, representing the same or different item but oriented vertically. Participants then pressed a key to indicate whether the second image corresponded to the result of their MR of the first image.

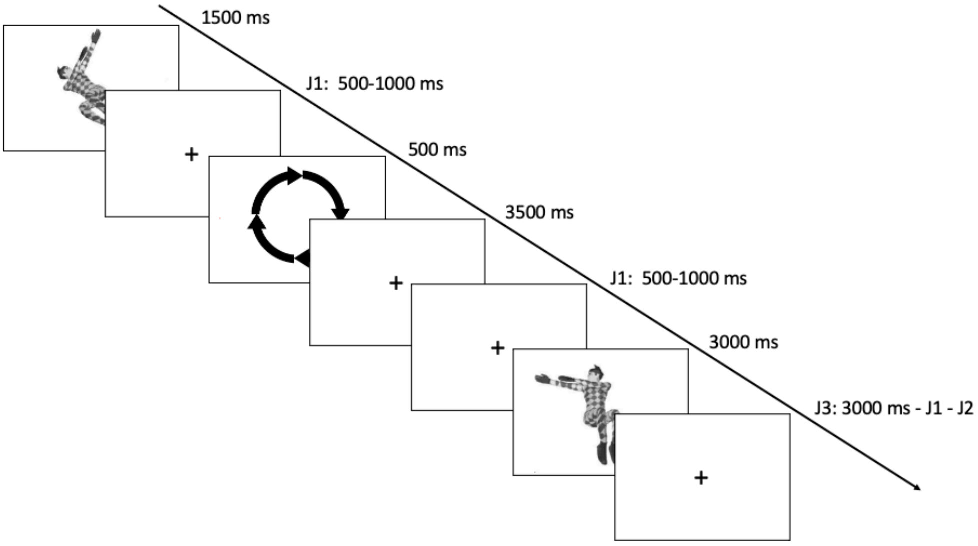

**Figure 2 – Example of experimental trial.** Participants were asked to mentally rotate the first image in the direction given by the arrows until reaching the vertical. Then participants indicated whether the second image represented the same or different item with respect to the first image. In the example, the correct response is “different”.

In 50% of the cases, the answer was "same", and in 50% of the cases the answer was "different". To avoid memorization, the "different" trials were further divided into two categories: "mirrored" (as in Figure 2) or "wrong rotation". The 3 types of images were presented in a randomized order. In order to familiarize with the task, participants underwent a training session of four trials for each type of images outside the scanner.

The images used in the training session were different with respect to those used in the experiment.

### *4.3.4 MRI acquisition*

We used a Siemens Magnetom Prisma Fit 3 T scanner and a 64-channel head coil (Siemens, Erlangen, Germany) at the University Hospital's MR Center in Lausanne, Switzerland, to aquire both functional and anatomical images. A T2*-weighted echo-planar imaging sequence employing an isotropic voxel size of about 2 mm3, echo time/repetition time (TE/TR) of approximately 30/2000 msec, 64 slices, simultaneous multislice factor of approximately 2, field of view (FoV) of approximately 192 mm2, flip angle of approximately 80~, matrix size of approximately 96 ~ 96, interleaved ascending acquisition, and 2136 Hz bandwidth per pixel was applied to get the functional images. The field of view was aligned parallel with the commissural line and included the whole cerebrum. Dummy scans were acquired to establish steady-state magnetizations prior to each functional acquisition. To account for spatial distortion in the functional images, we acquired a pair of spin echo images with opposite phase encoding directions, matching the orientation of the functional scans. These spin echo images were obtained at the beginning of each run, for a total of 3 sequences. All images were presented using PsychoPy (psychophysics software in Python (Peirce et al., 2019) and delivered through MRI-compatible mirror attached to the head coil. For each of the six runs of the MR task, we collected 171 functional image volumes (6 min 20 s), including 6 additional volumes for safety purposes. To synchronize code and scanner, the functional acquisition initiated the presentation code. Anatomical images were acquired using a T1-weighted magnetization prepared rapid gradient echo (MP2RAGE) sequence (Marques et al., 2010), isotropic voxel size = $1mm^3$, FoV = 256 $mm^2$, TE/ $TR_{mprage}$ = 2.9/5000 msec, 192 contiguous sagittal slices, inversion time (TI1)/flip angle = 700 msec/4°, TI2/flip angle = 2500 msec/5°, matrix size = 240 x 240, duration = 3 min and 30 seconds.

We additionally recorded RT and accuracy during the runs. Data were stored in .txt files to be evaluated post-hoc.

### *4.3.5 Data analysis*

#### Behavioral data

We collected RT and accuracy data. Responses were filtered for errors and RT outliers above/below 3 standard deviations from the group mean specific for each type of image. Statistical analyses were performed with RStudio (https://rstudio.com/), comprising repeated-measure analyses of variance of the mean RTs and accuracy, with gender as a fixed factor and image as a random factor. Main effects and interactions were considered significant according to a level of significance of .05. If a significant effect was found, post-hoc analyses were performance using t-tests with the p-values adjusted for multiple comparisons according to the Bonferroni method.

#### MRI Quality Assessment Process

MRI data were converted using the Dcm2Bids program (https://github.com/cbedetti/Dcm2Bids) from DICOM format to the Brain Imaging Data Structure (https://bids.neuroimaging.io/). The MRI Quality Control tool (Esteban et al., 2017) was then used to assess the quality of the structural and functional data. Using the MRIQCeption tool (https://github.com/elizabethbeard/mriqception), a comparison was done between the acquired quality metrics and a set of metrics from the MRI Quality Control tool online application program interface (Esteban et al., 2019).

#### MRI data preprocessing

The fMRI data were preprocessed using fMRIPrep version 1.5.1rc2 (Esteban et al., 2019) a based on Nipype (Gorgolewski et al., 2011). The T1-weighted (T1w) volumes underwent intensity non-uniformity correction using N4BiasFieldCorrection (Tustison et al., 2010) distributed with ANTs 2.3.3 (Avants et al., 2008) and used as T1-weighted-reference throughout the workflow. They were then skull-stripped using antsBrainExtraction.sh v2.2.0, based on the Open Access Series of Imaging Studies (OASIS) template. Brain surfaces were reconstructed using recon-all from FreeSurfer v6.0.1 (Dale et al., 1999), and the brain mask obtained previously was further refined with a customized approach reconciling ANTs-derived and FreeSurfer-derived segmentations of the cortical gray matter from Mindboggle (Klein et al., 2017). To achieve spatial normalization, data were registered to the International Consortium for Brain Mapping

(ICBM) 152 Nonlinear Asymmetrical template version 2009c (Fonov et al., 2009) using the antsRegistration tool of ANTs v2.2.0 (Avants et al., 2008). This registration involved brain-extracted versions of both the T1w volume and the template. Subsequently, brain tissue segmentation for cerebrospinal fluid (CSF), white matter (WM), and gray matter (GM) was performed on the brain-extracted T1w data using fast (FSL v5.0.9; Zhang et al., 2001). The functional data underwent slice time correction using 3dTshift from AFNI v16.2.07 (Cox, 1996) and motion correction using mcflirt (FSL v5.0.9; Jenkinson et al., 2002). Distortion correction was performed using an implementation of the TOPUP technique (Andersson et al., 2003) with 3dQwarp (AFNI v16.2.07; Cox, 1996). Co-registration to the corresponding T1w data was done using boundary-based registration (Greve & Fischl, 2009) with six degrees of freedom, employing bbregister (FreeSurfer v6.0.1). The transformations for motion correction, field distortion correction warp, BOLD-to-T1w transformation, and T1w-to-template (MNI) warp were combined and applied in a single step using antsApplyTransforms (ANTs v2.2.0) with Lanczos interpolation.

To handle physiological noise, a Component Based Noise Correction Method (CompCor, Behzadi et al., 2007) was used to extract principal components for the anatomical CompCor variants (aCompCor). A mask excluding cortical signal was created by eroding the brain mask, leaving only subcortical structures. Six aCompCor components were calculated within the intersection of the subcortical mask and the union of CSF and WM masks derived from the T1w data, projected to the native space of each functional run. Frame-wise displacement (FD) and the Derivative of RMS variance over voxels (DVARS, Power et al., 2014) were calculated for each functional run using the Nipype implementations.

Further processing involved masking the functional data using the brain mask obtained from fMRIPrep. Fourteen fMRIPrep-derived confounds (six motion parameters, FD, standardized DVARS, and six aCompCor components) were removed at a voxel-wise level using the Denoiser tool (Tustison et al., 2010). Finally, the functional data were spatially smoothed using a Gaussian kernel with a full-width at half-maximum of 6 mm.

### First-level GLM analysis

For the first-level General Linear Model (GLM) analysis, FSL FEAT was used (www.fmrib.ox.ac.uk/fsl). A separate GLM model was constructed for each participant and each run, where the three images (abstract cubes, bodily figures, real objects) served as the regressors of interest, and their temporal derivatives were included as regressors of no interest. The regressors were convolved with a double-gamma hemodynamic response function and timed with the beginning and end of the video stimulus. We used FMRIB's Improved Linear Model (FILM) pre-whitening to adjust for autocorrelation, and a high-pass filter with a 100-second cutoff was used to remove low-frequency drifts.

### Group-level GLM analysis

Using mixed effects (FLAME 1) as implemented in FSL, a whole-brain group-level analysis was performed to determine mean group effects. A cluster-based method was used to threshold the statistical map, with a threshold of $Z > 2.3$. Family-wise error correction was then applied to make adjustments at $p = 0.05$.

### Univariate analysis

In order to study precisely the time windows during which MR was performed, we isolated the period of interest as the one following the cue, for a duration of 4 seconds.

Six separate contrasts were created to examine the distinctive neural activations corresponding to each image type, with group added as a regressor to determine whether any observed effects were influenced by the gender using two-sample unpaired t-tests. To investigate potential links with accuracy, this covariate was added in a separate model. Accuracy was mean centered by subtracting the overall mean accuracy from each individual score and added as a third explanatory variable in the model, for both positive and negative effect.

## 4.4 Results

### *4.4.1 Behavioral results*

The analysis of accuracy data revealed the significant main effects of gender [$F(1,165)=5.93, p=.015^{*}, \eta^2=0.03$] and image [$F(2, 165) = 10.10, p<.0001^{*}, \eta^2=0.11$]. The main effect of gender indicated that men had significantly higher scores than women (Figure 3). Post-hoc analyses of the main effect of image revealed that accuracy for the MR of real objects was significantly higher than MR of both abstract objects [t(1,110)=-4.65, p<.001***, d=-0.87] and bodily figures [t(1,111)=-3.61, p=.01**, d=-0.49] (Figure 4).

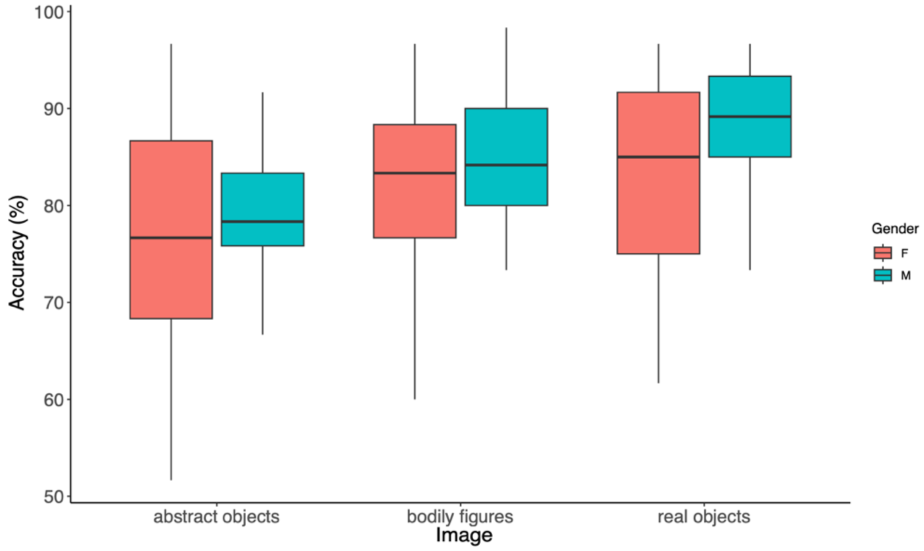

**Figure 3 - Accuracy across image types and separated by gender**. Analysis of variance revealed that men scored significantly higher than women.

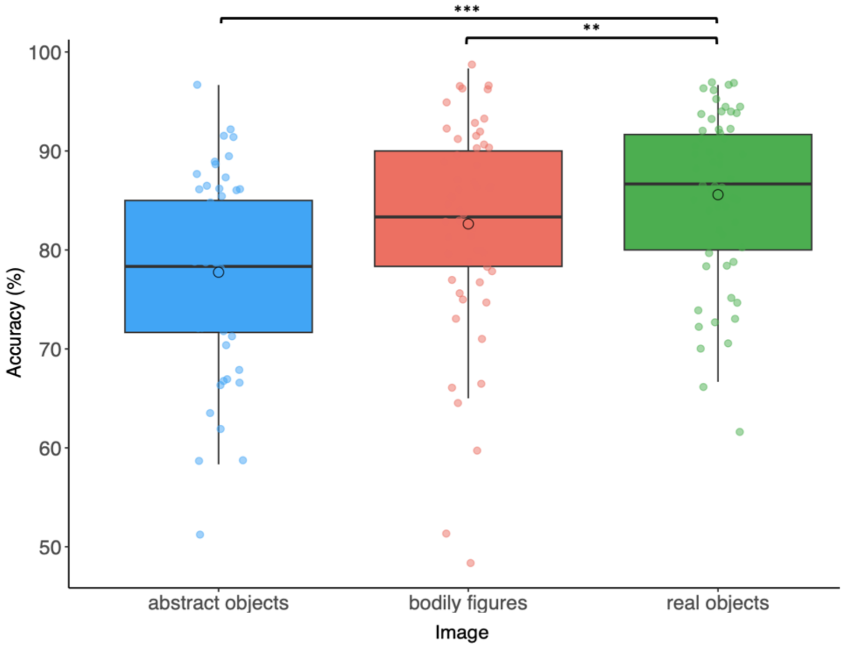

**Figure 4 - Accuracy** - Bonferroni-corrected t-tests revealed that participants were significantly less accurate in MR of abstract objects with respect to bodily figures and real objects. **Notes a significant difference p < 0.01. ***Notes a significant difference p < 0.001.

The analysis of RTs revealed the significant effect of image [*F*(2,165)=50.02, *p*<.001*, $\eta^2$=0.37]. Bonferroni-corrected post-hoc t-tests showed that MR of bodily figures took longer than abstract [*t*(2,103) = -7.25, *p*<.001***, *d*=-1.35] and real objects [*t*(2,102) = -9.00, *p*<.001***, *d*=-1.68].

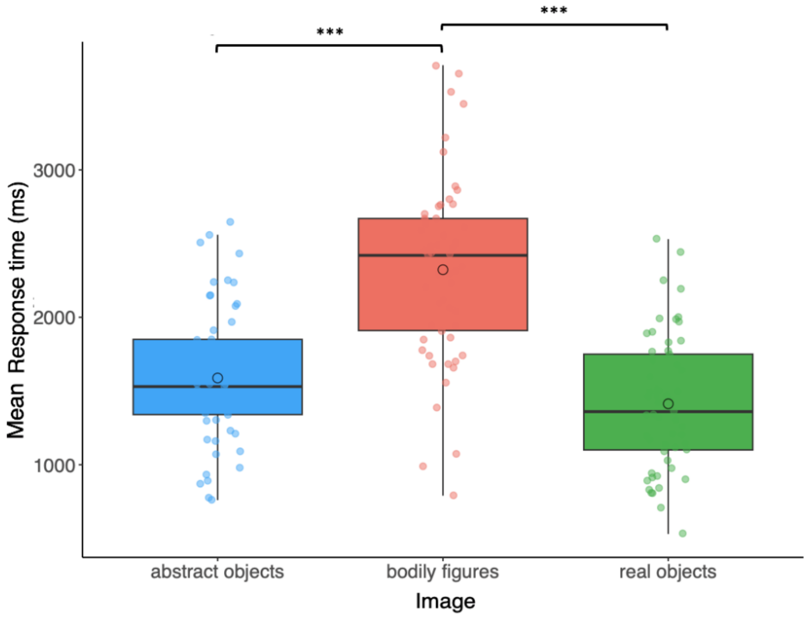

**Figure 5 - Response time.** Bonferroni-corrected t-tests of the significant main effect of image revealed that MR with bodily images was significantly slower with respect to abstract and real objects. ***Notes a significant difference p < 0.001.

### *4.1.2 Neuroimaging results*

The significant group contrasts for men and women during MR of abstract objects, bodily-figures and real objects are summarized in Table 1.

### **Gender-specific brain activity**

For the MR of abstract objects, men had higher activity than women in a cluster covering the right inferior frontal lobe and the middle frontal lobe (peak coordinates =

48, 38, 12; peak t-value = 4.55, 630 voxels in the cluster), in the triangular part (Figure 6; Table 1). Conversely, no significant clusters resulted more activated in women compared to men. For the MR of bodily figures, men had stronger activity than women in two main clusters: 1) one comprising the right superior medial frontal lobe, the anterior cingulum, and a small portion of the left superior medial frontal lobe (peak coordinates = 0, 56, 22; peak t-value = 3.62, 434 voxels in the cluster); 2) another one located in the right superior medial frontal lobe (peak coordinates = 12, 60, 34; peak t-value = 3.38, 387 voxels in the cluster) (Figure 6, Table 1). No significant clusters resulted more activated in women than men. There were no gender differences in the brain activity associated with MR of real objects.

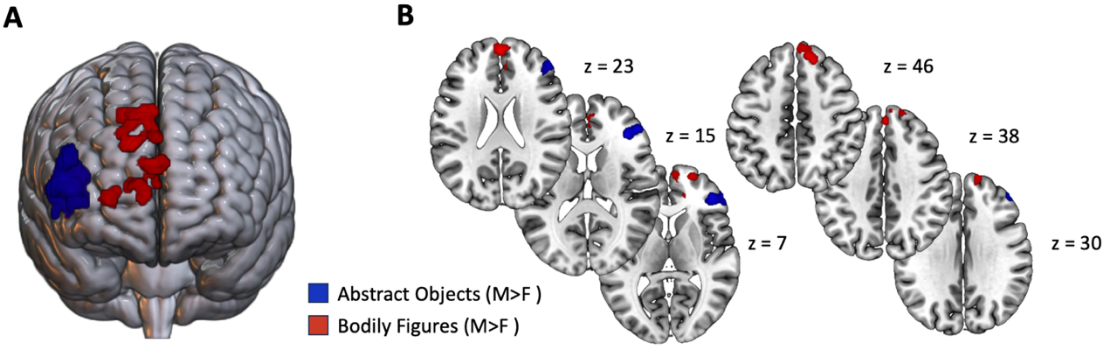

**Figure 6 – Gender-specific brain activity associated with MR of different images.** The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The activation clusters represent the brain regions where men had higher activation compared to women for the MR of abstract objects (blue) and bodily figures (red). These statistical maps were assessed with a cluster-based threshold of Z > 2.3 FWE-corrected at p = 0.05.

### Gender-Image interactions

Contrasting the brain activity related to MR of bodily figures against abstract objects, women showed stronger activation in the right inferior-superior parietal cortex lobe (peak coordinates = 40, -50, 42; peak t-value = 3.4, 614 voxels in the cluster) and the bilateral precuneus lobe (peak coordinates = -2, 74, 58; peak t-value = 3.59, 461 voxels in the cluster) (Figure 7, Table 1). The reverse contrast didn't reveal any cluster significantly more active in men compared to women. Contrasting the brain activity associated with MR of real objects versus bodily figures, women showed stronger activation in the right occipital pole lobe (peak coordinates = 34, -86, -10; peak t-value = 3.8, 412 voxels in the cluster), including the lingual gyrus (Figure 7, Table 1). The reverse contrast didn't show any activation significantly stronger in men than women.

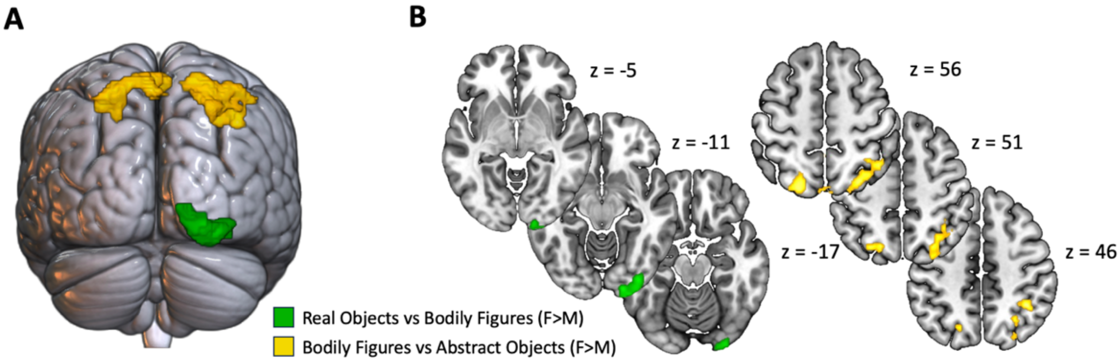

**Figure 7 – Brain activity-related relationships between gender and MR image.** The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The activation clusters represent the brain regions where women had higher activation compared to men in the contrast between MR of bodily figures and abstract objects (yellow) and between real objects and bodily figures (green). These statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, FWE-corrected at $p = 0.05$.

### Gender-Accuracy correlations

When accuracy was added as a regressor in the third level analysis, differences emerged for both women and men in the MR of real objects. For men, a positive relationship was found between the accuracy in MR of real objects and the activation of a cluster comprising the bilateral precuneus and superior occipital lobe (peak coordinates = -2, -52, 42; peak t-value = 3.55; 304 voxels). For women, a negative relationship was found between the accuracy in MR of real objects and the activation of 2 clusters: one comprising the right precentral gyrus lobe (peak coordinates = 30, -18, 64; peak t-value = 3.89; 3432 voxels in the cluster), and one covering the right premotor and supplementary motor areas, and the left paracentral lobule (peak coordinates = 10, -10, 70; peak t-value = 3.52, 362 voxels in the cluster, Figure 8, Table 1).

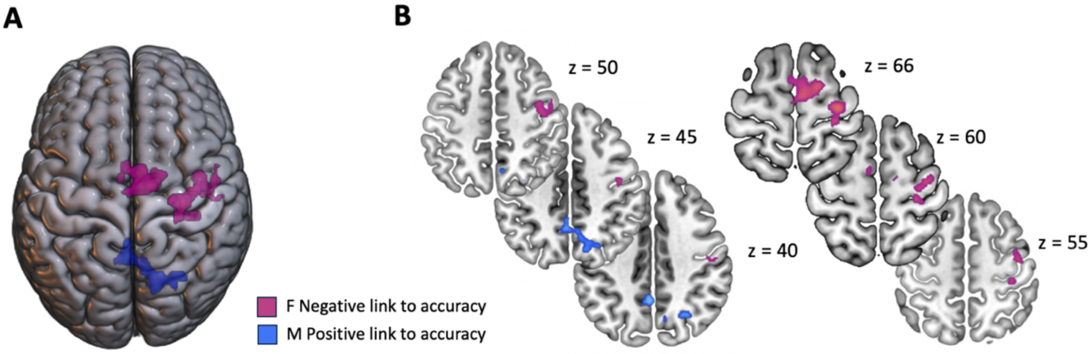

**Figure 8 – Correlation between MR-related brain activity and accuracy for real objects.** The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The activation clusters represent the regions where men's performance in MR of real objects positively correlated with their brain activity (blue) and women's performance in MR negatively correlated with accuracy (magenta). These statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, FWE-corrected at $p = 0.05$.

**Table 1. Significant clusters from whole brain**

| | | MNI | | Peak Z | Cluster level | |
|---|---|---|---|---|---|---|
| | x | y | z | | Size | p |
| **BODILY-FIGURES Males>Females** | | | | | | |
| L Superior Medial Frontal Lobe | 0 | 56 | 22 | 3.62 | 434 | 0.011 |
| R Anterior Cingulum | 16 | 42 | 10 | 3.27 | | |
| R Superior Frontal Lobe | 26 | 62 | 4 | 3.21 | | |
| R Superior Medial Frontal Lobe | 8 | 66 | 4 | 2.97 | | |
| R Superior Medial Frontal Lobe | 12 | 60 | 34 | 3.38 | 387 | 0.02 |
| **ABSTRACT OBJECTS Males>Females** | | | | | | |
| R Inferior Frontal Lobe | 48 | 38 | 12 | 4.55 | 630 | <.001 |
| R Middle Frontal Lobe | 38 | 32 | 16 | 4.25 | | |
| **BODILY-FIGURES vs. ABSTRACT OBJECTS Females>Males** | | | | | | |
| R Inferior Parietal Lobe | 40 | -50 | 42 | 3.4 | 614 | <.001 |
| R Superior Parietal Lobe | 26 | -68 | 58 | 3.16 | | |
| L Precuneus | -2 | -74 | 58 | 3.59 | 461 | 0.002 |
| R Precuneus | 4 | -48 | 62 | 3.26 | | |
| L Superior Parietal Lobe | -20 | -74 | 56 | 3.08 | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| **REAL OBJECTS vs. BODILY-FIGURES Females>Males** | | | | | | |
| R Inferior Occipital Lobe | 34 | -86 | -10 | 3.8 | 412 | 0.003 |
| R Lingual Gyrus | 20 | -94 | -12 | 3.77 | | |
| **REAL OBJECTS WITH ACCURACY AS A REGRESSOR MALES** | | | | | | |
| L Precuneus | -2 | -52 | 42 | 3.55 | 304 | 0.04 |
| R Superior Occipital Lobe | 28 | -64 | 40 | 3.23 | | |
| R Precuneus | 8 | -56 | 46 | 2.97 | | |
| **REAL OBJECTS WITH ACCURACY AS A REGRESSOR FEMALES** | | | | | | |
| R Precentral Gyrus | 30 | -18 | 64 | 3.89 | 432 | 0.01 |
| R Postcentral Gyrus | 28 | -26 | 62 | 3.07 | | |
| R Supplementary Motor Area | 10 | -10 | 70 | 3.52 | 362 | 0.03 |
| R Superior Frontal Lobe | 16 | -4 | 66 | 3.47 | | |
| L Supplementary Motor Area | -6 | -4 | 60 | 2.73 | | |
| L Paracentral Lobule | -4 | -14 | 72 | 2.53 | | |

## 4.5 Discussion

The present study shows that gender modulates the brain activity specifically associated with MR of different types of images (abstract objects, bodily figures, real objects): men and women differ in terms of both behavioral performance and brain activation patterns depending on the type of image being rotated. These findings demonstrate that gender differences in MR are highly dependent on the nature of the image being processed. While previous studies have examined the relationship between gender and MR using specific types of images, our study extends this line of inquiry by employing a broader range of stimuli. For example, Fisher (2018) focused on task complexity, showing that gender differences became less pronounced as MR stimuli become more realistic, but this work concentrated primarily on abstract objects made out of cubes. Rahe (2018) and Jansen (2020) further highlighted the importance of images' characteristics in driving distinct psychometric patterns in men and women. Our study advances this body of research by demonstrating that gender differences are not only image-dependent but also influenced by the degree of embodiment and the real-world familiarity of objects. By including real objects, we aimed to move beyond abstract and body-specific MR to explore how everyday items uniquely engage gender-specific neural networks. These differences indicated that the strategies employed during MR tasks—

whether visuospatial or motor-based—are influenced by the interaction between gender and the type of MR image.

### *4.5.1 Behavioral performance*

Behavioral results revealed gender differences, with men demonstrating greater accuracy than women in the MR task. This is in line with previous literature, which often shows a male advantage in tasks requiring mental manipulations of objects in space (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971; Voyer et al., 1995; Zapf et al., 2015). Recently, Zhang and colleagues (2024) put forward a novel hypothesis to explain these gender differences, investigating whether these disparities existed in large-scale brain networks associated with MR. When rotating abstract 3D cubes, men showed more intra-network integration and inter-network interaction in the salience network, which is thought to mediate interactions between multiple brain networks to influence mental activities (Menon & Uddin, 2010). Women on the other hand, exhibited higher inter-network interaction (i.e. higher inter-network connectivity and participation coefficient) of the visual network compared to men, potentially meaning that they may exert more effort to integrate low-level visual elements into mental imagery for complicated MR performance. This is consistent with our observation of greater activation of the right inferior frontal gyrus in men, which may reflect a greater reliance on visuospatial, object-based strategies to process and manipulate spatial information. It is also consistent with the observation of greater activation of the occipital gyrus in women, during MR of real objects compared to MR of bodily figures.

Results also showed differences in both accuracy and reaction times depending on the type of image used for MR. Participants showed higher accuracy in MR of real objects compared to bodily figures and abstract objects. This result is in line with previous evidence that mental spatial transformations of real objects is facilitated compared to other items. For example, Iachini and colleagues (2019) investigated behavioral patterns as a function of image type. The results showed that MR of concrete items (as hands and animal faces) shows lower errors rates than MR of abstract items. In addition, visual complexity seems to play an important part. As shown by Jordan et al. (2002), the difficulty of MR increases with visual complexity, in that participants show that MR is faster and more accurate for 2D letters with respect to 2D abstract shapes or 3D cubes.

Finally, also the familiarity of objects plays a significant role in modulating MR performance. For example, Doyle and Voyer (2018) explored the role of image familiarity and found that human figures, which are more familiar to participants than abstract block shapes, improved accuracy in MR tasks. Ruthsatz, Neuburger, Jansen, and Quaiser-Pohl (2014) concur with these findings, showing that fourth graders classified cube figures as masculine and similarly designed pellet figures as feminine. Based on this, they postulated that boys were more likely than girls to be familiar with cube figures because of their greater exposure to construction toys such as LEGO®. In their MR tests, there was no significant gender effect with pellet-figure items, and boys only outperformed girls on tasks involving cube figures rotated in-depth, concluding that a higher level of familiarity mediate the gender effect at least in tasks requiring in-depth rotations. They thus adhere to Koriat and Norman's (1985) hypothesis that greater familiarity with objects leads to the generation of "a broadly tuned memory representation that enables direct recognition of the stimulus over" a wide range of angle disparities (Koriat & Norman, 1985, p. 437). Altogether, we propose that our participants were more accurate with the MR of real objects because this type of images is more concrete, less visually complex, and more familiar compared to bodily figures and abstract objects.

Regarding RTs, the significant main effect of image showed that MR of bodily figures was significantly slower than abstract and real objects. This finding suggests that bodily figures might involve more complex cognitive processing, possibly due to the integration of both visuospatial and embodied processes. Krügger and colleagues (2014) came to the same conclusion in an MR experiment where participants were asked to mentally rotate body parts attached to abstract stimuli reflecting human possible and impossible postures, colored-end cubes, and simple-end cubes. Participants showed shorter RTs when deciding whether two rotated images were identical or not, and made less mistakes in MR of bodily figures in possible postures. They were however slower and less accurate in MR of bodily figures in impossible postures. The authors explained these results by hypothesizing that body parts automatically trigger embodiment, even in the case of impossible postures, where this is detrimental and significantly reduces performance. Such findings are not unanimous, however, as other studies have demonstrated facilitation by embodiment processes. For example, Amorim and colleagues (2006) and Jansen and colleagues (2020) observed that participants show shorter RTs and lower error rates in the MR of Shepard and Metzler's 3D cubes than MR of human figures. Conversely, Doyle et al. (2016) observed that participants were faster in the MR of human figures compared to 3D cubes. One possible explanation for these contradictory findings could lie in the influence of task instructions. Zacks et al. (2008) suggested that different MR strategies could be triggered by the way the task is explained to participants. When instructions emphasize the physicality or movement of the stimuli, participants might be more inclined to engage motor-based strategies, activating motor-related brain regions, even when a visuospatial strategy could be more effective. In studies such as those by Krügger et al. (2014) and Doyle and Voyer (2013), the instructions given to participants were not precisely detailed, which leaves ambiguity about whether the task setup may have unintentionally prompted participants to engage in motor imagery. In scenarios where bodily stimuli are highlighted as graspable or relatable, this could trigger embodiment processes that may increase cognitive load and result in slower reaction times. On the other hand, when the task is framed as a purely spatial manipulation, participants may rely more on visuospatial strategies, leading to faster and more efficient performance. Thus, the differences in how the MR task is presented or explained may account for the variability in findings across studies, suggesting that embodiment processes might be contingent on how participants approach the task. In our experiment, the instructions were relatively general, simply asking participants to "mentally rotate this figure". Judging by the significantly longer RTs, however, we can assume that a process of embodiment was at play, albeit not resulting in improved accuracy, thus corroborating results from Krüger and colleagues (2014).

### *4.5.2 Men-specific brain activity related to MR*

In the MR of abstract objects and bodily figures, the activation of the medial prefrontal cortex (mPFC) was higher in men than women. Within the fronto-parietal network involved in MR (Cohen et al., 1996; Schendan & Stern, 2007), PFC has been related to the monitoring aspects within the working memory needed to perform MR (Petrides et al., 1993) and is significantly more active while solving cognitive tasks strongly relying on MR, such as tangram puzzles (Çakır et al., 2011) and jigsaw puzzle pieces (Mutlu et al., 2020). Accordingly, greater negative amplitude in the PFC was linked to larger angular disparity between target images in a classic MR task (Yu et al., 2009).

Previous studies showed that mPFC is involved both in MR and self-referential thoughts. On the one hand, mPFC is important for visuo-spatial transformations related to MR (Johnston et al., 2004) MR of paired figures activates the frontal medial gyrus (Vingerhoets et al., 2001) and visual object cognition overlaps with the initial phase of MR in mPFC . On the other hand, mPFC plays a central role in self-referential thought (D'Argembeau et al., 2007; Gusnard et al., 2001; Mitchel et al., 2005) and, in particular, in Theory of Mind (Frith et al., 2003; Lev-Ran et al., 2012), the ability to understand and attribute mental states to oneself and others. Theory of Mind correlates with MR (Lehmann & Jansen, 2019), predict individual spatial abilities including MR (Viana et al., 2016) and, together with MR, is part of common age-specific stages of mental spatial transformation abilities (Frick et al., 2014). Importantly, transcranial electrical stimulation of mPFC improves Theory of Mind in women but not in men (Adenzato et al., 2017), suggesting that mPFC in men is already strongly involved in Theory of Mind. On this basis, we propose that the higher activity in mPFC shown by men in the present study may reflect a stronger reliance on self-related Theory-of-Mind-like reference frame in parallel with a stronger cognitive effort to perform MR. This mechanism would be further modulated by the manipulability of the object to be mentally processed, that it would come into force for abstract objects and bodily figures, which are less "manipulable" with respect to real objects. This would bring that, with respect women, men would more strongly rely on self-referred cognitive processing even if MR concerns relatively less manipulable objects.

During MR of abstract objects, men showed higher activity in the right inferior and middle frontal gyri compared to women. This finding is in line with previous evidence that men show stronger inferior frontal activations despite similar performance in cognitive tasks (Bell et al., 2006). The apparent controversy between studies showing that the MR-related activation of the inferior frontal gyrus is stronger in women than men (Hugdahl et al., 2006; Thomsen, Hugdahl, Ersland, Barndon, Lundervold, Smievoll, Roscher, et al., 2000) or in men than women (Semrud-Clikeman et al., 2012) might be biased by methodological issues such as small sample size (5 women and 6 men were include in both Hugdahl and Thomsen). In line with the findings of Semrud-Clikeman et al (2012), our results confirm that the activation of inferior frontal gyrus is stronger in men than women, further demonstrating that this pattern is specific for abstract objects, because it was absent in MR of real objects and bodily figures. Interestingly, we showed in a previous study that specifically comparing brain activations caused the use of a visuospatial strategy to a control condition to solve a MR task resulted in a significant cluster in the inferior frontal lobe (Bersier et al., 2024). This reinforces our belief that men are more inclined to use a visuospatial strategy, at least when it involves abstract shapes or human bodies.

Considering that the activation inferior frontal gyrus is associated with working memory (Baldo & Dronkers, 2006; Minamoto et al., 2010; Nixon et al., 2004; Rypma et al., 1999), and that working memory plays a central role in MR (Hyun & Luck, 2007; Lehmann et al., 2014; Pardo-Vazquez & Fernandez-Rey, 2012; Wang et al., 2018), we propose that the differential inferior frontal activation in men and women may reflect a different effort in working memory to perform MR of abstract objects, which would be higher in men than women. This interpretation would be corroborated by the gender difference in MR-related activation of the inferior frontal gyrus is associated with anatomical differences (Blanton et al., 2004; Hammers et al., 2007; Harasty et al., 1997; Tomasi & Volkow, 2012). Alternatively, it is possible that the inhibitory mechanisms needed to retain responding before MR is completed drive the gender differences in inferior frontal activation. In fact, men show greater inferior frontal activation during successful inhibition, while women show greater engagement during unsuccessful inhibition (Weafer, 2020). The present study suggests that women may employ more automatic cognitive processing in MR of abstract objects (less working memory).

### *4.5.3 Women-specific brain activity related to MR*

During MR of abstract objects and bodily figures, women had stronger activity in the superior parietal lobe, compared to men (Table 2, Figure 7). This cluster is consistent with the results of the meta-analysis by Tomasino and Gremese (2016), which compared the neural networks associated with the MR of different images or different strategies in MR. In their contrast comparing MR performed in an egocentric versus allocentric perspective, the superior parietal lobe was more active during egocentric strategies (Tomasino & Gremese, 2016). Neuroimaging studies have demonstrated increased superior parietal activation during MR tasks (Tagaris et al., 1996), especially in MR of objects (Harris & Miniussi, 2003). In the present study, the stronger superior parietal activation in women than men for MR of both abstract objects and bodily figures could reflect that women tend to use an egocentric strategy not only for images like bodily figure that hint toward egocentric cognitive processing related to embodiment, but also for MR of images representing abstract objects which may not require embodiment-like cognitive processing. This interpretation is in line with previous findings that women are more likely than men to use egocentric cognitive processing to solve MR tasks (Bersier et al., 2024), women tend to employ egocentric perspectives in MR of human-like stimuli (Muto, 2021), and that in women the egocentric MR of bodily images elicits stronger brain activation in regions related to body-based mental statial transformation (Seurinck et al., 2004).

In apparent contrast with this previous evidence that occipital regions are recruited during MR of specifically full body images (Blanke et al., 2010; Perruchoud et al., 2016; Zacks, 2008), we found that women showed higher occipital activity than men during MR of real objects compared to MR of bodily figures. However, since previous studies comprised both men and women in their samples, it could be possible that the obtained results were driven by eventual effects brought by only one part of the sample. Showing that in women the occipital regions were more activated during MR of real objects than bodily figures, our findings suggest that the localization of brain activity related to MR depends on gender. This finding suggests that the activity of a region like the occipital cortex that has been traditionally linked to MR of bodily images, can in fact encode MR of a different image (real objects) based on gender-related preferences. Since the activity in this region has been related to visuospatial processing, we propose that women prefer visuospatial strategies to perform MR of images (real objects) that otherwise would seem to recruit different strategies (likely sensorimotor) due to possible overpowering by men's brain activation in previous studies.

### *4.5.4 Correlation between MR accuracy and brain activity*

When accuracy was added as a regressor for the analysis of brain activation related to MR of real objects, we observed opposite effects for men and women.

In men, increased accuracy was related to increased activation in the precuneus, in the superior parietal lobule. The parietal cortex is associated with spatial information processing (Brázdil et al., 2007) and allocation of both bottom-up and top-down attention (Singh-Curry & Husain, 2009). The precuneus, in particular, is typically affiliated with MR (Barriga, 2015) and with the use of an object-based visuospatial strategies to solve

MR tasks (Boccia et al., 2014; Lambrey et al., 2012; Zhang & Ekstrom, 2013). This approach is often proposed to be more effective, because it is faster and less error-prone, compared to an effector-based strategy (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971). Some studies have hyped that men's superior performance in MR tasks could be explained by a spontaneous adoption of this strategy. Butler and colleagues (2006) for example, when comparing MR of abstract objects between men and women, found that men had a stronger activity in the precuneus, compared to women, while showing higher accuracy when rotating abstract figures. The precuneus has also been involved in viewpoint and array rotation tasks (Lambrey et al., 2012), where men show stronger activation in the precuneus and right inferior frontal gyrus than women in spatial perspective tasks women (Kaiser et al., 2008). On this basis, we propose that the correlation between accuracy and activity in the precuneus for the MR of real objects in men represents the employment of a visuospatial strategy to solve MR, which would not be the preferred strategy in women. Thus, the present finding suggests the existence of gender-specific neuro-behavioral patterns bound to the cognitive strategy adopted in MR tasks.

For women, there was a negative correlation between the performance in MR of real objects and the activation of the primary motor cortex and the supplementary motor area: the higher the motor activation the lower the accuracy. Motor regions are typically associated with the employment of motor strategies and an egocentric frame of reference to solve MR tasks (Bersier et al., 2024; Kosslyn et al., 1998; Vingerhoets et al., 2002). Our results seem to indicate that women tend to rely on motor strategies for the rotation of real objects. The reason for this can be explained in the light of the characteristics of this image category. Real objects have the particularity of being explicitly graspable, and have been selected with several criteria in mind, including being manipulable with just one hand. In this vein, Grèzes et al. (2003) showed how the intrinsic properties of an object affected motor responses that were either consistent or inconsistent with the action that the object allowed. Their results showed faster motor responses to objects that allowed a consistent grip, showing that graspable objects are treated differently at the cognitive level. For MR however, it seems that exploiting the motor properties of manipulable objects is not the best way to proceed. Our results support this idea that visually presented real objects automatically initiate some aspects of action simulation especially in women.

Moreover, Long, Fan and colleagues (2021) highlighted that gender differences in MR are mediated by the functional connectivity between the default mode network (DMN) and the salience network (SN). Men may rely more on visuospatial networks linked to the DMN and SN, while women may engage more motor-related processes, as indicated by the differences in accuracy and brain activity when rotating real objects in our study. In our case, we observed a negative correlation between accuracy and motor cortex activation in women during MR tasks involving real objects. This finding suggests that while motor areas are automatically activated, relying on motor strategies in these tasks may actually interfere with the efficiency of a visuospatial strategy, leading to decreased accuracy in women. This supports the hypothesis that action simulation triggered by graspable objects, while useful in some contexts, may not always be the most effective strategy for MR tasks, particularly in women.

## 4.6 Conclusion

In conclusion, our study offers new insights into the interaction between stimulus (image), gender, and MR performance. Our findings demonstrate that gender modulates the different behavioral outcomes and neural activations related to different type of stimuli. The use of egocentric (body-based) or visuo-spatial (object-based) cognitive strategies to perform MR differ between women and men as a function of the type of image. Furthermore, the observed gender differences in the correlation between accuracy in MR and brain activity. Altogether, the nuanced understanding of how different types of stimuli engage distinct cognitive processes and brain regions offers a novel contribution to the ongoing discussion about the role of gender in MR tasks.

# Chapter 5

## Experiment 4:

## Cognitive traits shape the brain activity associated with mental rotation

Manuscript submitted to Cerebral Cortex. All the materials related to this paper (stimuli, data, and code for data analysis) are publicly available at the following GitHub repository: https://github.com/nadiaBRS/Cognitive-traits-shape-the-brain-activity-associated-with-mental-rotation

### 5.1 Abstract

Mental rotation (MR) is a fundamental spatial cognitive ability that is influenced by several factors, including cognitive traits. This study investigates the relationship between MR performance, cognitive traits (visual-verbal style, perspective taking, and cognitive flexibility), and brain activity using functional magnetic resonance imaging (fMRI). Fifty-five participants (27 females) aged 19-35 completed MR tasks with 3D abstract pictures, bodily pictures, and manipulable objects during fMRI scanning. Participants also completed the Object-Spatial Imagery Questionnaire (OSIQ), the Cognitive Flexibility Scale, and a perspective taking test. Behavioral data (accuracy and reaction time) and neuroimaging data were analyzed to assess the impact of cognitive traits on MR performance and brain activation patterns. Behavioral analysis revealed that spatial visualizers outperformed object visualizers in MR tasks, showing higher accuracy and faster reaction times. Perspective taking ability was also positively correlated with MR performance. Neuroimaging results indicated that individuals with lower MR performance showed greater brain activation, particularly in motor and sensorimotor

regions, supporting the neural efficiency hypothesis. Spatial visualizers, who performed better on MR tasks, showed more localized and reduced brain activation compared to object visualizers. The study highlights the influence of cognitive traits on MR performance and brain efficiency, with spatial visualizers showing more efficient neural processing. These findings contribute to our understanding of how cognitive styles shape spatial cognition and suggest potential for training interventions to enhance MR abilities and neural efficiency.

## 5.2 Introduction

One of the most fundamental human cognitive abilities is spatial cognition (Schaie, 1996). By asking participants to imagine and identify a two- or three-dimensional object rotated at a specific angle from its original upright position, the so-called mental rotation (MR) test is an established visuospatial task that can be used to assess spatial cognition (Cooper & Shepard, 1973; Riecanský & Jagla, 2008). Many factors are known to influence MR, such as gender (Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971; Voyer et al., 1995; Zapf et al., 2015), sex hormones (Bernal et al., 2020; Bernal & Paolieri, 2022; Courvoisier et al., 2013; Gurvich et al., 2023; Hausmann et al., 2000; Moffat & Hampson, 1996; O'Connor et al., 2001; Scheuringer & Pletzer, 2017), experience (Hertanti et al., 2019; Jansen & Pietsch, 2010; Terlecki et al., 2008), top-down strategies (Bersier et al., 2024; Halpern, 2013; Linn & Petersen, 1985; Shepard & Metzler, 1971) or bottom-up effects (Amorim et al., 2006; Ionta et al., 2013; Kosslyn et al., 1998; Tomasino & Gremese, 2016, Bersier et al.2024, in review).

Recently, there has been a surge of interest as to whether, on top of demographic variables, psychological factors like cognitive traits may play a central role in influencing MR. Cognitive traits are ways of acquiring and processing information which regulate individual cognitive functioning (Klein, 1951). They are stable throughout life and influence attitudes, strategies, preferences, ways of perceiving and learning information (Jonassen & Grabowski, 1993). It is therefore natural to ask whether the way we perceive and respond to the information around us would influence our performance on a cognitive task such as MR.

A cognitive trait that may play an important role in MR is the visual cognitive style, hinting to individual preferences for processing visual information. People with a visual cognitive style tend to engage in mental imagery even when presented with words (Bendall et al., 2016). The visual cognitive style can be further divided into object and spatial visualization cognitive styles. These styles are largely uncorrelated and associated with different abilities and preferences (Haciomeroglu & LaVenia, 2017). Object visualizers excel in picture recognition, while spatial visualizers perform better in mental spatial transformation (Kozhevnikov et al., 2013). Neuroimaging evidence supports the distinction between object- and spatial-visualizers, in that different brain activity patterns are associated with each cognitive style (Motes et al., 2008). These two visual cognitive styles are associated with measurable differences in MR tasks (Vandenberg & Kuse, 1978), with spatial visualizers being more accurate and faster than object visualizers.

Another cognitive trait that may influence the performance on MR tasks is perspective taking, defined as the ability to reorient oneself and take the perspective of another person or object (Hegarty & Waller, 2004). The available evidence suggests a complex relationship between perspective taking and MR abilities. While MR and perspective taking are highly correlated (Geva & Henik, 2019), they appear to involve different cognitive processes. Perspective taking tasks often require larger angular changes (>90°) and are generally more challenging than MR tasks (Geva & Henik, 2019). Both abilities contribute to spatial navigation performance, with perspective taking uniquely predicting variance in tasks requiring updates to self-to-object representations (Kozhevnikov et al., 2006). Three basic elements are involved in perspective taking tasks: 1) an object or circumstance upon which the perspective is taken; 2) a perspective-taker (self), who judges another's perspective; 3) a target (other) perspective that can be judged (an imagined self-perspective, a directional object, or another person). Surtees and colleagues (2013) suggested that perspective taking reflects the ability to engage in MR. The consequent hypothesis would be that the better the visual perspective taking, the better the performance in MR.

Finally, MR seems to be related to cognitive flexibility, the trait that reflects our ability to adapt our behavior and thinking in response to complex and novel situations (Ionescu, 2012). People that exhibit high cognitive flexibility are able to think creatively beyond pre-existing frameworks, view things from various angles, and adjust swiftly to changing conditions. In this sense, Nazareth and colleagues (2019) recently explored this issue by tracking participants' eye movements during a MR task and highlighted two different eye patterns – fixation and switching patterns. The latter, reflecting the alternation between strategies (i.e. flexible strategy), was associated with a better MR performance and may be indicative of the ability to select an optimal behavior based on task difficulty.

Such a proven influence of cognitive traits on MR hints to the possibility that also the brain activity associated with MR may be affected by cognitive traits. However, this question has not been addressed yet. In the present study, we investigated the relationship between MR performance measured in response time (RT) and accuracy, cognitive traits (perspective taking, visuo-verbal style, cognitive flexibility) and brain activity (functional magnetic resonance imaging; fMRI), using an event-related design in fMRI. We predicted that higher and lower scores in visual cognitive style, perspective taking, and cognitive flexibility, respectively would be associated with different accuracy in MR and different patterns of brain activity. Furthermore, based on the principle of economy, we predicted that lower accuracy on the MR task would be associated with increased brain activity. Based on our previous findings (Bersier et al., 2024; Bersier et al., submitted), we predicted that additional activations would be found in motor and sensorimotor regions.

## 3.4 Materials and Methods

### *3.4.1 Participants*

Sixty participants were recruited via local online platforms and social media. Five participants were excluded from the final sample (three due to poor MR performance, and two due to bad performance in the perspective taking task). The final sample consisted of 55 participants (27 females, age 24.33±4.15 years, range 19-35; 28 males, age 25.29±4.25 years, range 20-35). Prior to the experiment, participants gave their written consent and completed a safety questionnaire for the fMRI environment. Participants then completed the Object-Spatial Imagery Questionnaire (OSIQ; Blajenkova et al., 2006) to measure visual-verbal style, performed the perspective taking test (as described below), and were assessed through the Cognitive Flexibility Scale (CFS; Martin & Rubin, 1995). The following exclusion criteria were applied: age outside of the pre-determined range (18–35 years); uncorrected visual impairment; neurological or psychiatric disorder; incompatibility with fMRI settings; left-handedness, as defined by scores below the 60-

point cut-off on the Edinburgh Handedness Inventory (Oldfield, 1971). The experimental procedures were approved by the local ethics committee and the experiment was conducted in accordance with the Declaration of Helsinki (2013).

### *3.4.2 Visual Cognitive Style*

The Object-Spatial Imagery Questionnaire (OSIQ) is a 30-item self-assessment tool created to evaluate how individuals differ in their visual imagery preferences and experiences (Blajenkova et al., 2006) The OSIQ includes two distinct subscales: The object subscale measures object visualization, which gauges the preference for processing vivid images of objects; The spatial subscale measures spatial visualization, which measures the preference for understanding schematic spatial relationships. On the basis of the OSIQ score, each participant was classified as either "object-visualizer" or "spatial-visualizer", with an additional score (high, low) within each scale object-scale, spatial-scale).

### *3.4.3 Perspective taking test*

To measure perspective taking abilities, we used the Spatial-Orientation Test (Hegarty & Waller, 2004, Kozhevnikov & Hegarty, 2001), which is able to assess the ability to mentally simulate spatial transformations of one's own orientation and perspective. This test is a widely recognized tool for measuring spatial orientation abilities, particularly how individuals can position themselves within a given environment. The test consists of 20 items, each printed on a separate page. For each item, participants are shown an array of images at the top of the page, along with an "arrow circle" at the bottom, which includes a specific question regarding the spatial relationship between the images. Participants are instructed to imagine themselves standing at a particular image in the array, designated in the center of the arrow circle, and facing another image, indicated at the top of the circle. From this imagined viewpoint, participants must determine the direction toward an object and draw an arrow from the center of the circle to indicate this direction. To ensure participants understand the task, a practice trial was provided prior to the test. In this practice trial, participants were asked to imagine standing at a flower (center image, first) and facing a tree (top image, second). The correct direction toward a cat (object image, third) was already marked with an arrow, demonstrating the correct procedure. Participants were encouraged to ask questions if they did not fully understand the task. Throughout the test, participants were instructed not to pick up or turn the test booklet and to refrain from making any marks on the image arrays. The focus was on accurately determining directions while avoiding excessive time spent on every single trial.

### *3.4.4 Cognitive flexibility*

The CFS (Martin & Rubin, 1995) is a 12-item questionnaire used to assess how flexible individuals are in their thinking and behavior (e.g., "I can communicate an idea in many different ways;" "I seldom have choices when deciding how to behave"). Participants are instructed to read each statement and respond by selecting how much they agree or disagree with the statements, rating their answer from 1 to 6 as following: 6 = strongly agree, 5= agree, 4= slightly agree, 3= slightly disagree, 2= disagree, 1=strongly disagree. The average score among students has been reported around 55 points.

### *3.4.5 MR Stimuli*

Participants performed MR of 3 distinct images (abstract objects, human bodies, and real objects) during the recording of fMRI data (Figure 1). Abstract objects comprised 6 pictures that resembled the ones used by Shepard and Metzler (1971). The 6 human body images showed a complete body in 6 different postures (curtesy of Amorim et al., 2006). The 6 real objects represented a motorbike break, a wrench, a stapler, a corkscrew, a spray bottle, and a can opener. Digital manipulation was used to ensure that all images had the same overall size, symmetry, and absence of writing.

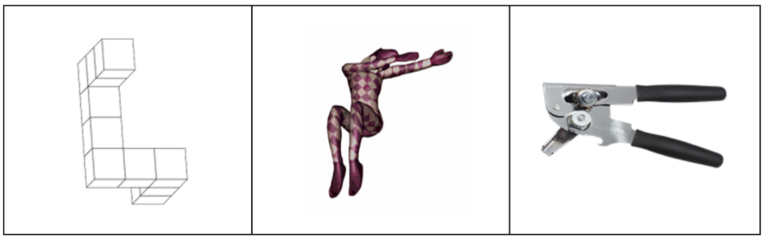

**Figure 1 – Experimental stimuli** consisted in images of abstract objects, human bodies, and real objects.

### *3.4.6 Procedure*

During fMRI data recording, participants performed an MR task (Bersier et al. in press). Sixty image pairs were presented to the participants. The first image in each pair displayed an image (abstract object, human body, real object) rotated with respect to the vertical by one of ten different rotation angles (±30°, ±60°, ±90°, ±120°, and ±150°). This first image was displayed for 1.5 seconds, followed by a jittered blank screen that lasted between 0.5 and 1 second. A circular arrow rotating in either a clockwise or counterclockwise direction served as the cue for 500 milliseconds, after which a screen flashed the word "GO" for 3.5 seconds. During this time, participants were asked to mentally rotate the first image until the vertical position. They pressed a key to indicate when they finished the task (RT). Upon receiving the participant's response, the "GO" screen flickered on and off for 0.5 to 1 seconds. Then, the second image of the pair was shown for 2.5 s, representing the same or different item of the first image, but oriented vertically.  Participants had to press a key to indicate whether the second image matched the result of the MR they performed on the first image.

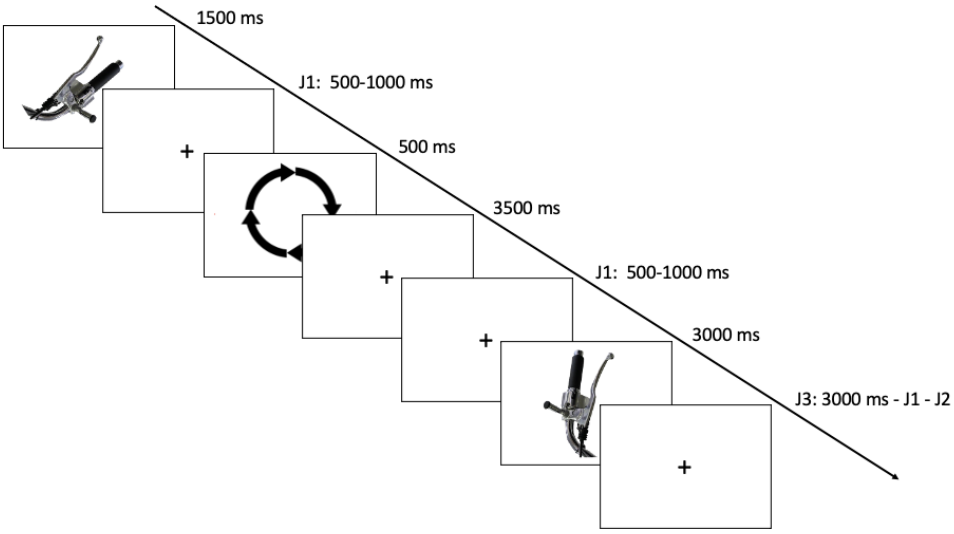

**Figure 2 – Example of experimental trial.** Participants were asked to mentally rotate the first image in the direction given by the arrows until reaching the vertical. Then participants indicated whether the second image represented the same or different item with respect to the first image. In the example, the correct response is "different" (the first is right, the second is left).

In 50% of the cases, the answer was "same", and in 50% of the cases the answer was "different". To avoid memorization, the "different" trials were further divided into two categories: "mirrored" (as in Figure 2) or "wrong rotation". The 3 types of images were presented in a randomized order. To familiarize with the task, participants underwent a training session of four trials for each type of images outside the scanner. The images used in the training session were different with respect to those used in the experiment.

### *3.4.7 MRI acquisition*

We used a Siemens Magnetom Prisma Fit 3 T scanner and a 64-channel head coil (Siemens, Erlangen, Germany) to acquire both functional and anatomical brain images. A T2*-weighted echo-planar imaging sequence employing an isotropic voxel size of about 2 mm$^3$, echo time/repetition time (TE/TR) of approximately 30/2000 msec, 64 slices, simultaneous multislice factor of approximately 2, field of view (FoV) of approximately 192 mm2, flip angle of approximately 80~, matrix size of approximately 96 ~ 96, interleaved ascending acquisition, and 2136 Hz bandwidth per pixel was applied to get the functional images. The field of view was aligned parallel with the commissural line and included the whole cerebrum. Five dummy scans were acquired to establish steady-state magnetizations prior to each functional acquisition. To account for spatial distortion in the functional images, we acquired a pair of spin echo images with opposite phase encoding directions, matching the orientation of the functional scans. These spin echo images were obtained at the beginning of each condition, for a total of 3 sequences. All the images of the MR task were administered with PsychoPy (psychophysics software in Python; Peirce et al., 2019), projected on a screen behind the fMRI scanner, and viewed by the participants through a mirror attached to the head coil. For each item of the MR task, participants' RT and accuracy were automatically recorded. For each of the six runs of the MR task, we collected 171 functional image volumes (6 min 20 s), including 6 additional volumes for safety purposes. To synchronize code and scanner, the functional acquisition initiated the presentation code. Anatomical images were acquired using a T1-weighted magnetization prepared rapid gradient echo (MP2RAGE) sequence (Marques et al., 2010) , isotropic voxel size = 1mm$^3$, FoV = 256 mm$^2$, TE/ $TR_{mprage}$ = 2.9/5000 msec, 192 contiguous sagittal slices, inversion time (TI1)/flip angle = 700 msec/4°, TI2/flip angle = 2500 msec/5°, matrix size = 240 x 240, duration = 3 min and 30 seconds.

### *3.4.8 Data analysis*

#### Behavioral data

Items with RTs above 3 standard deviations from the group mean for each image category (abstract objects, human bodies, real objects) were excluded from the analysis. Statistical analyses were performed with RStudio (https://rstudio.com/). Repeated measures analyses of variance were performed to explain the mean RT and accuracy, with the factors stimulus (abstract objects, human bodies, real objects), OSIQ style (object-visualizer, spatial-visualizer), and OSIQ scores (high, low), perspective taking performance (high, low), cognitive flexibility (high, low). The high or low classification for each assessment was determined by the participant's position relative to the group median. As object- and spatial-visualizers groups were not balanced in terms of size (N=41 for object-visualizers and N=14 spatial-visualizers), another division within the scales was made, resulting in "high/low score on the object scale" and "high/low score on the spatial scale". The score for the perspective taking test was computed by calculating the difference in degrees between what the subject drew and what the correct answer is for the item, either in the clockwise or counterclockwise direction. Therefore, the higher the score, the worse the performance. For clarity throughout the paper, this quote has been inverted to avoid confusions. Therefore, an original high score to the perspective taking test has been classified as low performance and vice versa. Main effects and interactions were considered significant according to a level of significance of .05. If a significant effect was found, post-hoc analyses were performance using t-tests. *P*-values were adjusted for multiple comparisons according to the Bonferroni method.

#### Brain Imaging Quality Assessment Process

Functional and anatomical brain images were converted from the Digital Imaging and Communications in Medicine (DICOM) format to the Brain Imaging Data Structure (BIDS; https://bids.neuroimaging.io/) using the Dcm2Bids program (https://github.com/cbedetti/Dcm2Bids). To evaluate the quality of both structural and functional brain images, the MRI Quality Check (MRIQC; Esteban et al., 2017) tool was employed. Additionally, a comparative analysis was conducted using MRIQCeption (https://github.com/elizabethbeard/mriqception), which involved comparing the acquired quality metrics with a reference dataset obtained from the MRIQC online Application Programming Interface (Esteban, Blair, et al., 2019).

## MRI data preprocessing

Preprocessing of the fMRI data was carried out using fMRIPrep version 1.5.1rc2 (Esteban, Blair, et al., 2019), built on Nipype (Gorgolewski et al., 2011). The T1-weighted (T1w) images were first corrected for intensity non-uniformity using N4BiasFieldCorrection (Tustison et al., 2010), available with ANTs version 2.3.3 (Avants et al., 2008). These corrected images served as the T1-weighted reference for subsequent steps. Skull-stripping was performed using antsBrainExtraction.sh v2.2.0 based on the OASIS template, followed by the reconstruction of brain surfaces through the recon-all command from FreeSurfer v6.0.1 (Dale et al., 1999). The brain mask was further refined by integrating ANTs and FreeSurfer segmentations of the cortical gray matter, utilizing a customized approach informed by Mindboggle (Klein et al., 2017).

For spatial normalization, the data were aligned to the International Consortium for Brain Mapping 152 Nonlinear Asymmetric template version 2009c (Fonov et al., 2009) via the antsRegistration tool of ANTs v2.2.0 (Avants et al., 2008), utilizing brain-extracted versions of both the T1w volume and the template. Segmentation of brain tissues, including cerebrospinal fluid, white matter, and gray matter, was performed using fast (FSL v5.0.9; Zhang et al., 2001). Functional data were corrected for slice timing with 3dTshift from AFNI v16.2.07 (Cox, 1996) and for motion using mcflirt (FSL v5.0.9; Jenkinson et al., 2002). Distortion was addressed with a TOPUP-based approach (Andersson et al., 2003) implemented in 3dQwarp (AFNI v16.2.07; Cox, 1996). Co-registration of functional data to the T1w images was performed using boundary-based registration (Greve & Fischl, 2009), with six degrees of freedom, via the bbregister function (FreeSurfer v6.0.1). All transformation steps, including motion correction, field distortion adjustment, BOLD-to-T1w alignment, and T1w-to-template (MNI) registration, were applied in one step using antsApplyTransforms (ANTs v2.2.0) with Lanczos interpolation.

To reduce physiological noise, a Component Based Noise Correction Method (CompCor; Behzadi et al., 2007) was employed. A subcortical mask was created by eroding the original brain mask, and six aCompCor components were derived from the intersection of this mask with the union of cerebrospinal fluid and white matter masks generated from T1w images. These components were projected onto the native space of each functional run. Additionally, frame-wise displacement and the derivative of RMS variance over voxels (DVARS; Power et al., 2014) were computed for each run using Nipype.

Subsequent processing steps involved masking the functional data based on the brain mask provided by fMRIPrep. Fourteen confounding variables from fMRIPrep (including six motion parameters, frame-wise displacement, standardized DVARS, and six aCompCor components) were regressed out at the voxel level using the Denoiser tool (Tustison et al., 2010). The final step involved spatial smoothing of the functional data using a Gaussian kernel with a 6 mm full-width at half-maximum.

### First-level GLM analysis

For the first-level General Linear Model (GLM) analysis, FSL FEAT was used (www.fmrib.ox.ac.uk/fsl). A separate GLM model was constructed for each participant and each run, where the three images (abstract cubes, human bodies, real objects) served as the regressors of interest, and their temporal derivatives were included as regressors of no interest. The regressors were convolved with a double-gamma hemodynamic response function and timed with the beginning and end of the video stimulus. We used FMRIB's Improved Linear Model pre-whitening to adjust for autocorrelation, and a high-pass filter with a 100-second cutoff was used to remove low-frequency drifts.

### Univariate analysis

In order to study precisely the time windows during which MR was performed, we isolated the period of interest as the one following the cue, for a duration of 4 seconds.

Using two-sample unpaired t-tests, 6 separate contrasts were created to examine the distinctive neural activations corresponding to each condition, with group added as a regressor to determine whether any observed effects were influenced by the OSIQ style (object or spatial visualizer), the accuracy of MR performance, or by obtaining a “high” or “low” in the concerned cognitive trait (OSIQ subscales, perspective taking, cognitive flexibility). To investigate potential links with accuracy, this covariate was added in a separate model. Accuracy was mean centered by subtracting the overall mean accuracy from each individual score and added as a third explanatory variable in the model, for both positive and negative effect.

## 3.5 Results

### *3.5.1 Behavioral results*

**Accuracy**

The analysis of variance on MR accuracy revealed the significant main effects of stimuli [*F*(2, 157) = 11.38, *p*<.001], OSIQ style [*F*(1,157)=9.81, *p*=.002], OSIQ score on the spatial scale [*F*(1,157)=4.75, *p*=.03], score on the object scale [*F*(1,157)=4.03, *p*=.04] and score at the perspective-taking test [*F*(1,157)=4.52, *p*=.03]. No effect arose for the CFS score, neither did any significant interaction between factors. Post-hoc t-tests corrected for multiple comparisons showed a significant difference between the abstract objects and human bodies [*t*(1, 107) = 2.8, *p*=0.005] and between the abstract objects and real object images [*t*(1, 107) = 4.65, *p*<0.001] (Figure 4).

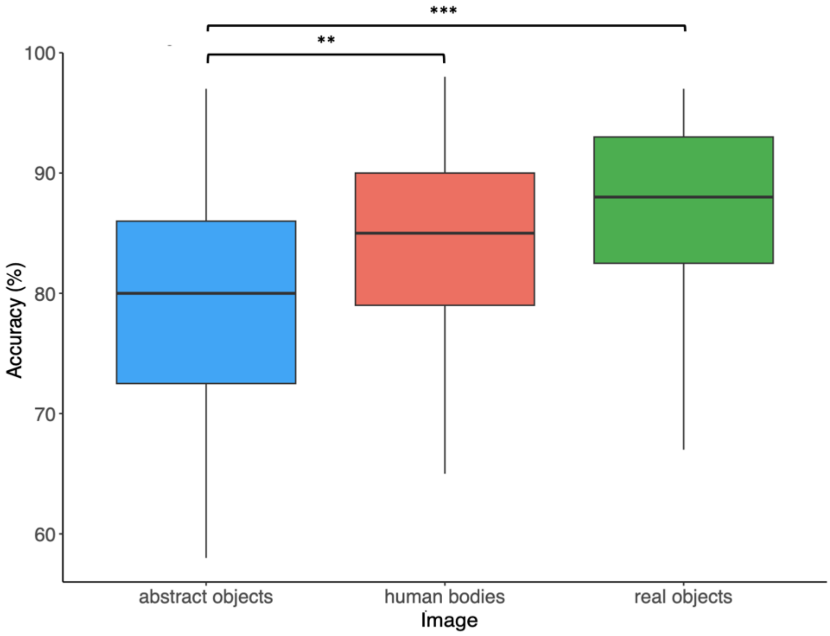

**Figure 4 – MR Accuracy**. Bonferroni-corrected t-tests revealed significant differences between the MR of abstract objects and human bodies, as well as between MR of abstract and real objects. **Notes a significant difference $p < 0.01$. ***Notes a significant difference $p < 0.001$.

Regarding the effect of the OSIQ style, spatial-visualizers were more accurate than object-visualizers (Figure 5).

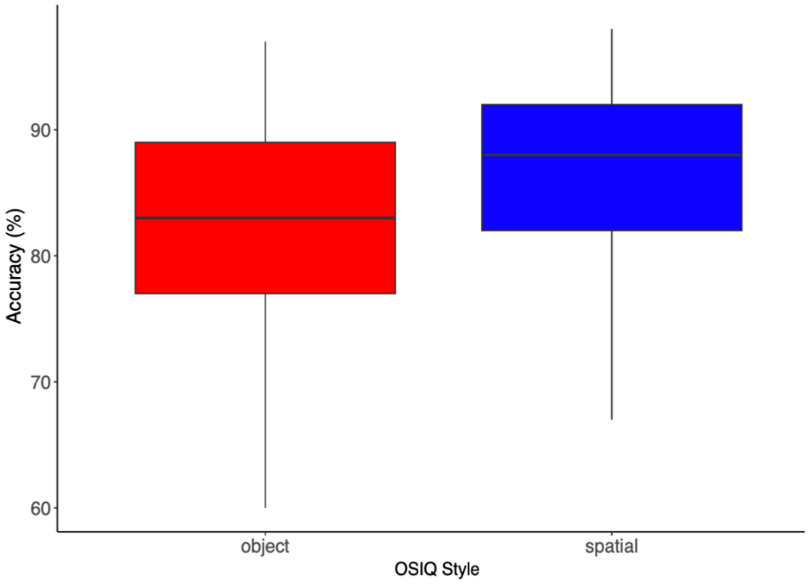

**Figure 5 – Accuracy according to the OSIQ style (object or spatial).** The spatial group scores were significantly higher on the MR task compared to the object group.

When dividing groups according to their score on the spatial scale of the OSIQ questionnaire, results corroborated the previous findings, as people presenting high score on the spatial scale exhibited greater accuracy at the MR compared to people presenting low scores on the scale (Figure 6).

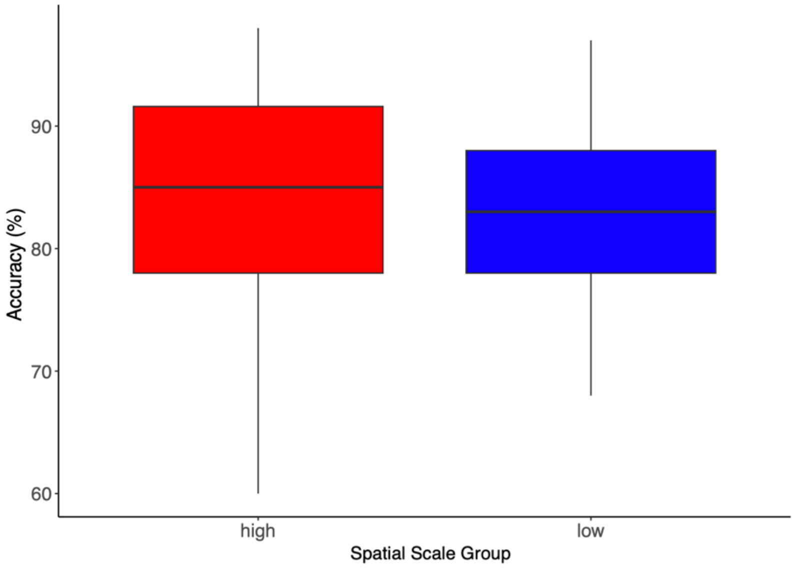

**Figure 6 – Accuracy according to the spatial scale group** (high score or low score). The high score spatial group present significantly higher accuracy at the MR task compared to the low score spatial group.

When dividing groups according to their score on the object scale of the OSQIV questionnaire, results corroborated the previous findings, as people presenting high score on the object scale exhibited lower accuracy at the MR compared to people presenting low scores on the scale (Figure 7).

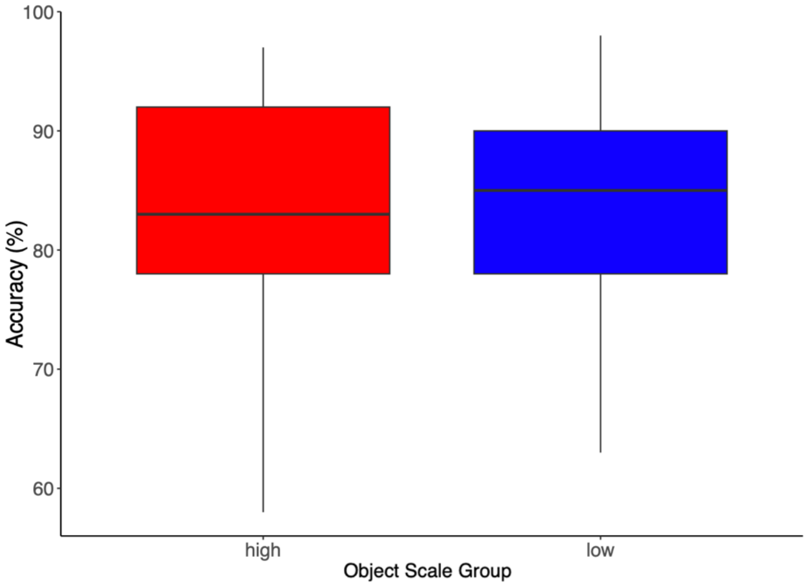

**Figure 7 – Accuracy according to the object scale group (high score or low score).** The high score object group present significantly lower accuracy at the MR task compared to the low score object group.

### Response Time

The analysis of variance on MR RTs revealed the significant main effects of stimulus [*F*(2, 157) = 50.10, *p*<.001] and OSIQ style [*F*(1,157)=7.3, *p*=.007]. Post-hoc t-test revealed that RTs for the human bodies were significantly longer compared to the abstract objects [*t*(1, 99) = 7.03, *p*<0.001] and real objects [*t*(1, 99) = 8.77, *p*<0.001] (Figure 8).

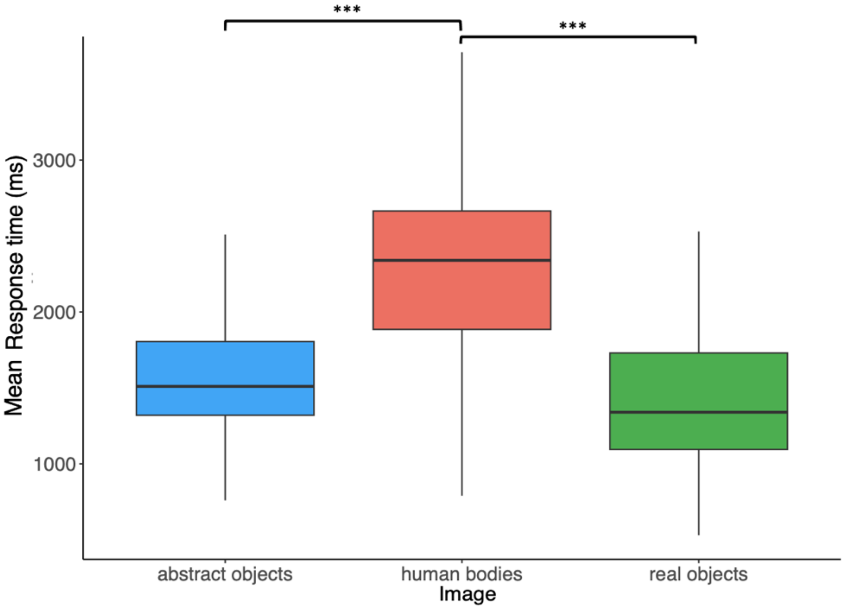

**Figure 8 – RTs across images.** T-tests (corrected for Bonferroni) revealed significant differences between the human bodies and abstract objects, as well as between the human bodies and real objects. ***Notes a significant difference p < 0.001.

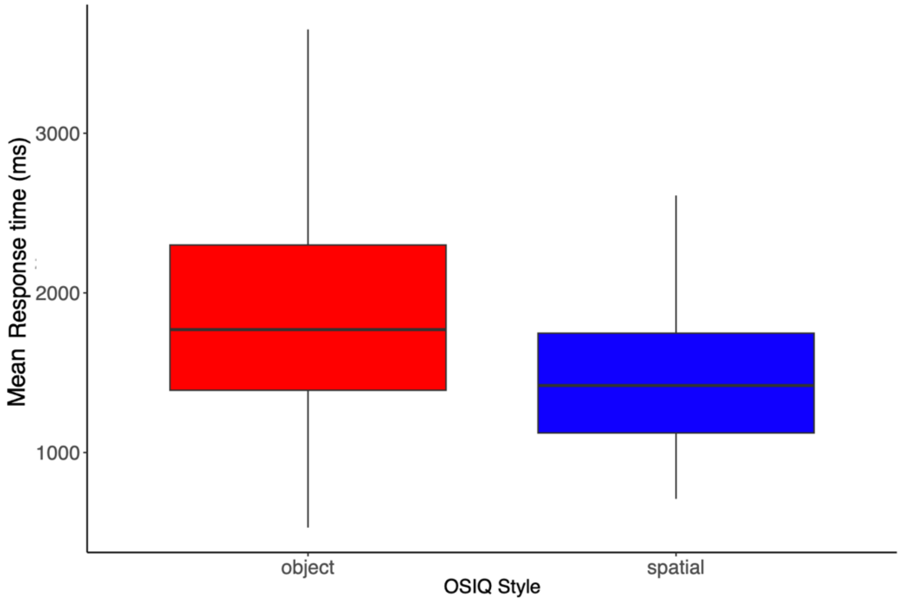

**Figure 9 – Mean RT according to the OSIQ style (object or spatial).** The spatial group scores shows significantly shorter RTs on the MR task compared to the object group.

### *3.5.2 Neuroimaging results*

**Mental Rotation**

During MR of human bodies, with respect to participants with high MR accuracy, participants with low accuracy in MR had stronger activity in four clusters located in the left hemisphere and comprising, respectively, (i) the middle occipital lobe and angular gyrus, (ii) the middle frontal gyrus, (iii) the precentral gyrus and opercular part of the inferior frontal lobe, and (iv) the superior frontal gyrus and supplementary motor area (Figure 10, Table 1). During MR of abstract objects condition, with respect to participants with high MR scores, those with low MR scores showed stronger activity in a cluster covering the left parietal and occipital lobe, angular gyrus (Figure 10, Table 1). The two contrasts overlapped in the angular gyrus.

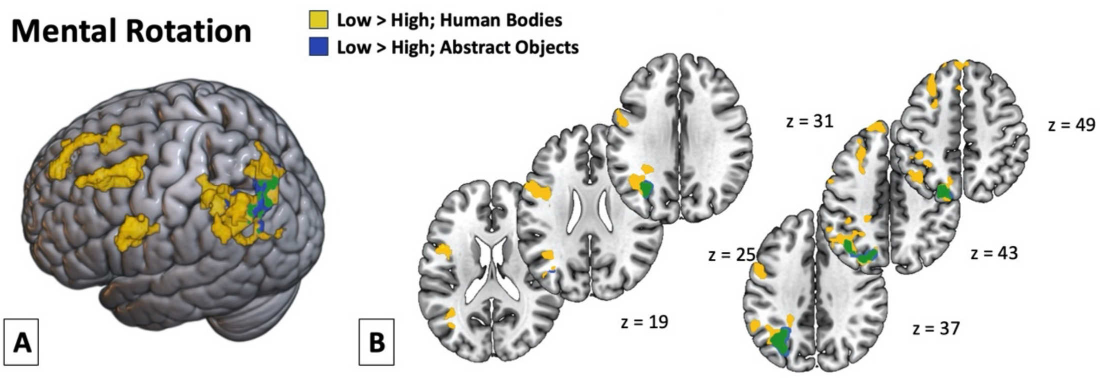

**Figure 10 – Stimulus-specific brain activity related to MR performance**. The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The activation clusters represent the regions where, with respect to participants with high scores in MR, participants with low scores in MR had stronger activations during MR of abstract objects (yellow) and human bodies (blue). The statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, corrected at $p = 0.05$ (family-wise error correction).

### Visual-cognitive style

The brain activity associated with MR of human bodies was different between object- and spatial-visualizers, as classified by the OSIQ. Object-visualizers showed stronger brain activity in a cluster comprising the primary motor and somatosensory cortices (Figure 11, Table 1). In addition, during MR of abstract objects, the object-visualizers had stronger activity in three clusters comprising (1) the left superior frontal gyrus and the left anterior and middle cingulum, (2) the middle cingulum bilaterally, and (3) the left postcentral, precentral, and supramarginal gyri (Figure 11, Table1).

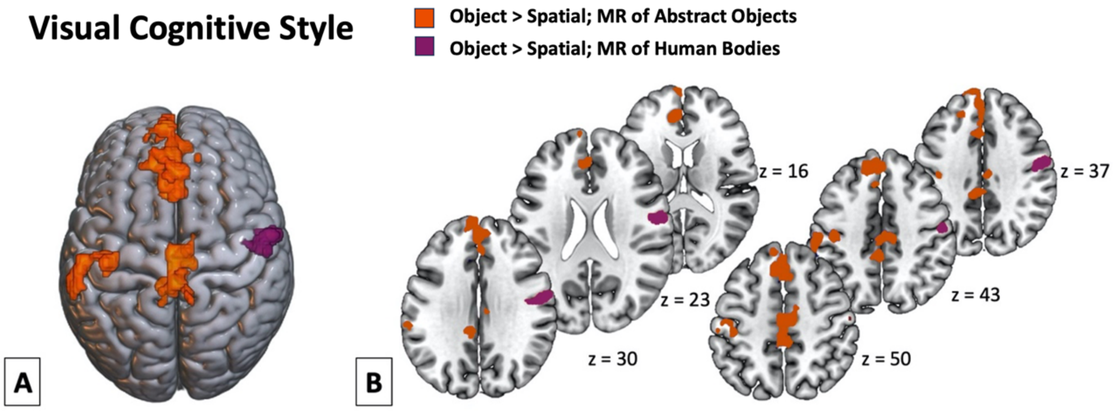

**Figure 11 – MR-related brain activity depending on Visual Cognitive Style (OSIQ).** The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The colored clusters represent the brain regions where the activity was significantly different between object-visualizers (Object) and spatial-visualizers (Spatial), with stronger activity in Object than Spatial, specifically during MR of human bodies (purple) and abstract objects (orange). These statistical maps were assessed with a cluster-based threshold of $Z > 2.3$ FWE-corrected at $p = 0.05$.

### Object and Spatial subscales of OSIQ

The comparison of high and low scores separately for object and spatial subscales of OSIQ showed two main significant differences. First, with respect to low scoring object-visualizers, high scoring object-visualizers showed stronger activity in a cluster comprising the left superior and inferior parietal lobes and angular gyrus during MR of abstract objects compared to real objects (Figure 12, Table 1). Second, during MR of abstract objects compared to human bodies, with respect to high scoring spatial-visualizers, low scoring spatial-visualizers had stronger activity in a cluster covering the right angular gyrus, middle temporal lobe, and inferior occipital lobe (Figure 12, Table 1).

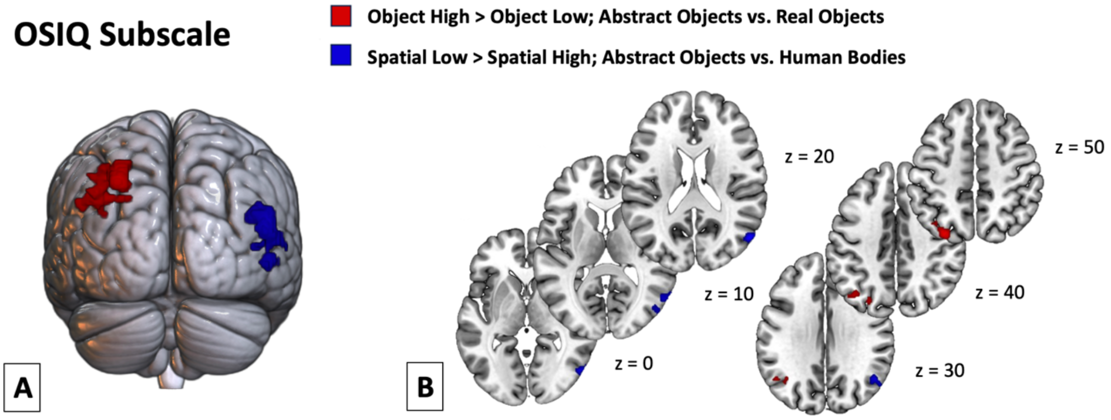

**Figure 12 – MR-related brain activity depending on OSIQ subscale**. The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). The colored clusters represent the brain regions where the activity was significantly different between participants that scored high and low in the respective subscale of OSIQ. Red clusters represent the regions where, compared to low scoring object-visualizers, high

scoring object-visualizers had stronger activity during MR of abstract than real objects. Blue clusters represent the regions where, with respect to high scoring spatial-visualizers, low scoring spatial-visualizers had stronger activity during MR of abstract objects than human bodies. The statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, corrected at $p = 0.05$ (family-wise error correction).

### Perspective Taking

During MR of abstract objects with respect to human bodies, low scoring participants in perspective taking had significantly stronger activity in two clusters, compared to participants with high scores in perspective taking. One cluster comprised the left the postcentral and precentral gyri, as well as the inferior parietal lobe. The second cluster included the supplementary motor area, the paracentral lobule, and the right middle cingulum (Figure 13, Table 1).

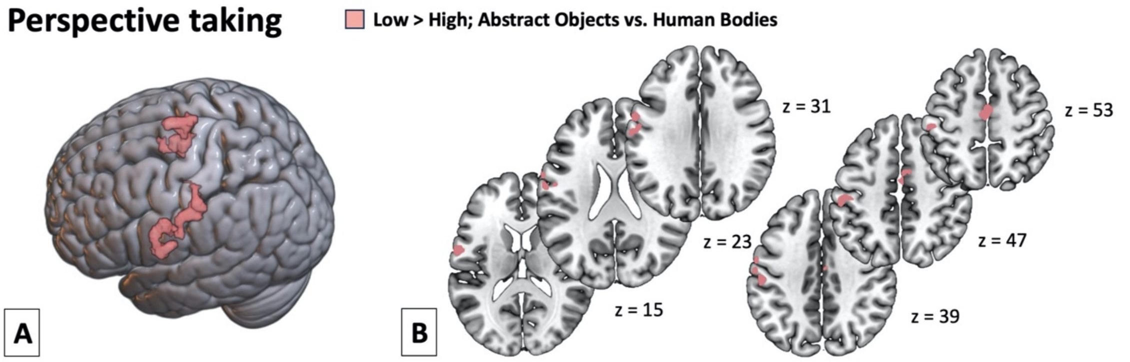

**Figure 13 – MR-related brain activity depending on perspective taking**. The results of whole-brain analysis are projected onto a 3D brain (A) and axial slices (B). Green clusters represent the regions where, compared to participants with high scores in perspective taking, participants with low scores in perspective taking had stronger activity during MR of abstract objects vs. human bodies. The statistical maps were assessed with a cluster-based threshold of $Z > 2.3$, corrected at $p = 0.05$ (family-wise error correction).

Table 1. Significant clusters from whole brain

| | BA | MNI | | | Peak Z | Cluster level | |
|---|---|---|---|---|---|---|---|
| | | x | y | z | | Size | *p* |
| **Human bodies low MR scorers > high MR scorers** | | | | | | | |
| L Angular Gyrus | 39 | -40 | -62 | 40 | 3.81 | 1663 | <.001 |
| L Middle Occipital gyrus | 39 | -36 | -62 | 34 | 3.67 | | |
| L Middle Frontal Gyrus | 8 | -30 | 24 | 52 | 3.93 | 477 | 0.006 |
| L Precentral gyrus | 6 | -50 | 2 | 22 | 3.66 | 443 | 0.01 |
| L Inferior Frontal lobe, Opercular part | 44 | -40 | 2 | 22 | 3.14 | | |
| L Superior Frontal gyrus | 8 | -14 | 50 | 46 | 3.56 | 349 | 0.04 |
| L Supplementary Motor area | 8 | -4 | 20 | 50 | 3.42 | | |
| L Superior Frontal Medial lobe | 8 | -2 | 36 | 58 | 3.4 | | |
| **Abstract objects low MR scorers > high MR scorers** | | | | | | | |
| L Middle Occipital lobe | 39 | -30 | -62 | 32 | 4.31 | 740 | <.001 |
| L Angular Gyrus | 39 | -40 | -64 | 40 | 3.47 | | |
| L Superior Parietal gyrus | 7 | -16 | -72 | 48 | 3.01 | | |
| **Abstract objects OV>SV** | | | | | | | |
| L Superior Frontal gyrus | 32 | -4 | 42 | 42 | 4 | 1299 | <.001 |
| L Anterior Cingulum | 32 | -8 | 42 | 16 | 3.84 | | |
| L Middle Cingulum | 32 | -4 | 20 | 36 | 3.8 | | |
| L Frontal Superior gyrus | 10 | -6 | 62 | 32 | 3.68 | | |
| L Middle Cingulum | 31 | -2 | -24 | 46 | 3.9 | 691 | <.001 |
| R Middle Cingulum | 24 | 8 | -20 | 44 | 3.89 | | |
| L Posterior Cingulum | 23 | -8 | -36 | 32 | 3.84 | | |
| L Postcentral gyrus, Primary sensory | 1 | -42 | -20 | 44 | 3.68 | 535 | 0.002 |
| L Supramarginal gyrus | 40 | -56 | -22 | 44 | 3.68 | | |
| L Precentral gyrus, Primary motor | 4 | -38 | -18 | 56 | 3.34 | | |
| L Inferior parietal gyrus | 40 | -60 | -28 | 44 | 3.14 | | |
| **OSIQ Object Scale HS > LS abstract objects vs. real objects** | | | | | | | |
| L Superior parietal lobe | 7 | -28 | -78 | 46 | 4.17 | 458 | 0.002 |
| L Angular gyrus | 39 | -38 | -64 | 36 | 3.28 | | |
| L Inferior parietal lobe | 7 | -34 | -62 | 46 | 3 | | |
| **OSIQ Spatial Scale low scorers > high scorers abstract objects vs. human bodies** | | | | | | | |
| R Angular gyrus | 39 | 48 | -60 | 26 | 3.98 | 401 | 0.006 |

|  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|
| R Middle temporal gyrus | 19 | 45 | -70 | 20 | 3.89 |  |  |
| R Inferior occipital lobe | 19 | 56 | -72 | -2 | 3.21 |  |  |
| **SOT low scorers>high scorers for abstract objects vs. human bodies** |  |  |  |  |  |  |  |
| L precentral gyrus | 6 | -60 | 2 | 28 | 3.3 | 416 | 0.004 |
| L Inferior parietal gyrus | 40 | -54 | -22 | 40 | 3.25 |  |  |
| L Rolandic operculum, Primary motor | 4 | -58 | -4 | 14 | 3.22 |  |  |
| L Postcentral gyrus, Primary motor | 4 | -62 | -8 | 20 | 3.15 |  |  |
| L Supplementary motor area | 6 | 0 | -10 | 54 | 3.83 | 389 | 0.007 |
| L Paracentral lobule | 6 | -2 | -16 | 72 | 3.69 |  |  |
| R Middle Cingulum | 32 | 4 | -2 | 44 | 2.95 |  |  |
| R Supplementary motor area | 6 | 12 | 4 | 46 | 2.44 |  |  |

## 3.6 Discussion

The present study investigated whether cognitive traits have a stimulus-specific influence on the neural and behavioral correlates of MR. To this aim we recorded brain activity while neurotypical participants performed MR of different stimuli (abstract objects, human bodies, and real objects), we measured their scores in 3 cognitive traits (visual-verbal style, perspective taking, cognitive flexibility), and we analyzed the covariance between cognitive traits and brain activity related to MR of different images. The results showed that the brain activity associated with MR was stimulus-specifically influenced by visual style and perspective taking, as well as by the performance level in the MR task.

### *3.6.1 Visual Cognitive style*

Our results showed that MR-related bran activity and performance were differentially influenced by object- versus spatial visual cognitive style. Participants identified as spatial-visualizers were faster and more accurate than object-visualizers, which is consistent with previous research suggesting that spatial visualizers are better equipped to handle the spatial manipulations required in MR tasks (Blajenkova et al., 2006; Kozhevnikov et al., 2005). This finding was corroborated by neuroimaging results, in that the stronger activity in sensorimotor and frontal regions shown by object-visualizers during MR of abstract objects, compared to spatial visualizers, was associated with lower overall accuracy. The larger brain activity could reflect a compensatory mechanism in which object-visualizers use additional neural resources to complete the task, such as additional top-down control (Barbey et al., 2011) or the use of a motor strategy (Tomasino & Gremese, 2016). This interpretation is in line with previous evidence that object- and spatial-visualizer may differentially recruit neural resources to accomplish the same tasks (Motes et al., 2008).

During MR of human bodies, object-visualizers showed a larger activation of the somatosensory cortex compared to spatial visualizers, suggesting that they may rely more on body-based processes to solve MR. This finding is congruent with previous evidence that larger sensorimotor activity during MR can be associated with lower accuracy (Bersier et al., 2024). Thus, the poorer accuracy of object-visualizers may be due to the involvement of sensorimotor regions. It is indeed well known that these regions are crucial for generating a kinesthetic image of the body in space and simulating body movements during MR tasks (de Lange et al., 2006; Maravita & Iriki, 2004; L. M. Parsons, 1994; Perruchoud et al., 2016). On this basis, we propose that object-visualizers' preference for vivid, concrete, manipulable images, may result in them being recruiting more concrete sensorimotor processes, which would not be as precise as visual ones. Thus, the activation of sensorimotor regions may interfere with the use of a purely spatial process, resulting in lower performance.

The lack of significant reverse contrast suggests that spatial visualizers showed more efficient neural processing, with less activation in the same regions, especially during the more complex human bodies and abstract objects images. This finding is in line with previous evidence that the preference for object-visualization style is linked to a more efficient utilization of cognitive resources, leading to reduced neural activity to perform object-related processing (Motes et al., 2008). These results suggest that spatial visualizers may have more optimized neural pathways for processing MR tasks, which may explain their superior performance at the behavioral level.

### *3.6.2 The influence of high and low scoring in visual cognitive style.*

Further results emerge when considering participants based on the basis of their individual scores on the object and spatial scales. Participants with high scores on the object scale showed a significantly stronger activity in the angular gyrus in the MR of abstract objects with respect to human bodies. The angular gyrus has been implicated in a variety of cognitive processes, including spatial reasoning (for a review, see Seghier, 2013) and MR. For instance, a damage to the angular gyrus is associated with impaired MR of letters (Doganci et al., 2024), the length of mental spatial transformations during MR of hands and chairs is associated with activity in the angular gyrus (Menéndez Granda et al., 2022), and the involvement of the angular gyrus in MR of real objects has been shown both in childhood and adolescence (Hirai et al., 2022). Furthermore, the angular gyrus is involved in detecting discrepancies between predicted and actual consequences of actions across different sensory modalities (van Kemenade et al., 2017), playing a critical role in integrating different sensory inputs for further cognitive processes (Bonner et al., 2013; Thakral et al., 2017; Tibon et al., 2019). Altogether, we propose that the stronger activity of the angular gyrus in high scoring object-visualizers, with respect to low scoring object-visualizers, may reflect a relatively larger effort to activate sensory simulation strategies to perform MR of abstract objects than human bodies. Considering that an affordance of abstract objects could be that they are seen as more "manipulable" than human bodies, we argue that participants with a higher tendency to focus on objects' features (high scoring object-visualizers) would need stronger mental efforts to perform the mental spatial transformations required by MR of items that, additionally, induce the mental simulation of the sensory inputs that would be generated by their physical manipulation. This mental effort would be reflected in higher brain activity of regions processing sensory inputs for further cognitive processing, such as the angular gyrus.

People who scored low on the spatial scale also showed an additional activation in the right middle temporal gyrus when the abstract objects was contrasted with the human bodies condition. The middle temporal gyrus and inferior temporal gyrus are involved in memory processing (Cabeza & Nyberg, 2000; Chao et al., 1999; Tranel et al., 1997), visual perception (Herath et al., 2001; Ishai et al., 1999), and multimodal sensory integration (Mesulam, 1998). The fact that people who score lower on the spatial scale also show additional brain activation in this area could mean that they rely relying more heavily on memory processes, visual perception, and multimodal sensory integration to compensate for their less efficient spatial processing abilities. This compensatory activation suggests that these individuals may be attempting to use alternative cognitive strategies, such as drawing on stored visual memories or integrating sensory information from multiple sources, to perform the mental rotation tasks. However, this reliance on additional neural resources may not be as effective as the more streamlined, spatially focused strategies used by those with higher spatial abilities, leading to their overall lower performance.

### *3.6.3 Perspective Taking*

Participants with higher perspective taking scores showed better accuracy on the MR task, with respect to participants with lower scores in perspective taking. This supports the notion that the ability to mentally adopt another perspective and manipulate spatial relationships is closely related to MR performance. In addition, the fMRI results showed that individuals with lower scores in perspective taking showed increased neural activity in motor brain regions, with respect to participants with high scores in perspective taking. These motor activations may reflect low scoring participants' greater effort to perform MR of items that have a stronger manipulation affordance, such as abstract objects with respect to human bodies. The recruitment of motor areas in participants with lower perspective-taking ability suggests that motor strategies may be used to achieve similar outcomes when cognitive reorientation is insufficient.

### *3.6.4 Cognitive Flexibility*

While previous studies have suggested that cognitive flexibility may influence strategy selection in spatial tasks (Nazareth et al., 2019), our study found no significant interaction between cognitive flexibility (measured through the CFS questionnaire) and MR-related performance nor brain activity. This discrepancy may be due to differences in task design or the specific aspects of how cognitive flexibility is measured. However, the lack of a significant effect in our study suggests that cognitive flexibility may not directly affect MR tasks, or at least not in the way originally hypothesized.

### *3.6.5 The role of the left angular gyrus*

The left angular gyrus was associated with lower performance in several of our contrasts and may be indicative of several underlying neural mechanisms. This region is known to play a critical role in spatial cognition, attention, and the integration of sensory information, making it essential for tasks requiring complex spatial processing (for a review, see Seghier, 2013). Increased activation in the left angular gyrus among lower performers in terms of accuracy in MR may reflect a compensatory effort to cope with the demands of the MR tasks. This increased activity may indicate less efficient processing, with the brain struggling to perform the necessary spatial transformations, resulting in greater cognitive load. In addition, the angular gyrus is involved in working memory and the allocation of attention, suggesting that individuals with lower performance in terms of accuracy may have difficulty maintaining and manipulating spatial information over time (Corbetta & Shulman, 2002; Wager & Smith, 2003). The overactivation observed in this region could also indicate a processing bottleneck, where the brain's attempts to integrate visual and spatial inputs become less effective, further contributing to the observed deficits in task performance (Marois & Ivanoff, 2005). Taken together, these findings suggest that the angular gyrus, while critical for spatial tasks, may become a site of inefficiency when overactivated, particularly in individuals with lower spatial abilities.

### *3.6.6 Neural efficiency*

A final general observation is that, in our study, a greater brain activation was always associated with less efficient performance on the MR task and seems to follow the neural efficiency hypothesis. The neural efficiency hypothesis suggests that individuals who perform better on cognitive tasks tend to show less brain activation, particularly in regions associated with task-relevant processing (Haier et al., 1992). This implies that their brains are working more efficiently, requiring less effort to achieve the same or better performance than those who perform less well, who often show increased brain activation. Several studies have used fMRI to investigate differences in brain activity between experts and novices, with experts showing lower or more localized brain activation during task performance compared to novices. For example, radiologists showed reduced activation in visual and non-visual brain regions during diagnostic tasks (Ouellette et al., 2020), while elite archers showed more localized neural activity in the dorsal pathway and cerebellum while aiming (Kim et al., 2014). In this sense, a parallel could be drawn between spatial visualizers and spatial expertise to explain our imaging results. Our results suggest that, similar to experts in other domains, spatial visualizers may possess more efficient neural networks that allow them to perform MR tasks with greater efficiency, thereby requiring less widespread brain activation. This reduced activation may indicate that their cognitive processes are more streamlined, allowing them to process spatial information with minimal effort. Conversely, object visualizers and those with lower MR performance may need to recruit additional neural resources, reflecting a less efficient cognitive strategy that requires more effort and results in increased brain activation. Thus, our results not only confirm the neural efficiency hypothesis in the context of mental rotation but also extend it by highlighting the role of cognitive styles in determining the efficiency of brain function during spatial tasks.

These findings have important implications for understanding the neural and cognitive mechanisms underlying MR performance. The differential brain activation patterns observed between spatial and object visualizers provide evidence for the existence of distinct cognitive and neural strategies in spatial tasks. This could inform future interventions aimed at improving MR performance, particularly in individuals who struggle with spatial visualization.

## 3.7 Limitations

A possible limitation is that cognitive traits were evaluated on the basis of self-reports (OSIQ, CFS). While these tools are widely used and validated, they are subject to biases related to subjective perception, including over- or under-estimation of abilities due to factors like self-awareness, social desirability, and item interpretation. This reliance on self-reports can lead to discrepancies between reported cognitive styles or flexibility and the actual strategies or behaviors used during tasks. In addition, cognitive styles and flexibility are complex constructs that may not be fully captured by these questionnaires alone. Future research should consider the use of objective measures, such as behavioral task, to complement self-report data and provide a more accurate and comprehensive assessment.

## 3.8 Conclusions

The present study investigated the relationship between cognitive traits such as object-spatial visual style, perspective taking, and cognitive flexibility and MR-related brain activity and performance.

Our findings show that participants with a spatial visualization style outperformed those with an object visualization style. This performance difference was further corroborated by neuroimaging data, in that object visualizers exhibited activations possibly related to mental effort, particularly when dealing with complex stimuli like abstract objects and bodies. These findings suggest that object visualizers may rely more on compensatory neural mechanisms, possibly due to their preference for concrete, manipulable images, which may interfere with pure spatial processing and reduce overall efficiency of the MR task.

Lower perspective taking scores were associated with lower accuracy in MR and higher activity in motor regions, suggesting the employment of motor-based simulation strategies to mentally rotate items with a stronger manipulability affordance.

Cognitive flexibility did not significantly influence MR-related performance nor brain activity. This finding suggests that only some specific cognitive traits affect MR, while cognitive flexibility may play a role in other cognitive domains.

At the neural level, the left angular gyrus was consistently associated with poorer performance across several analyses, suggesting that increased activation in this region may reflect compensatory efforts to manage the demands of MR tasks. This increased activity could indicate less efficient processing, as the brain struggles to integrate visual and spatial inputs, leading to greater cognitive load and reduced task performance.

Overall, our findings highlight the importance of some specific cognitive traits in shaping spatial cognition and support the neural efficiency hypothesis in the context of MR. These findings may inform future interventions aimed at improving MR performance, particularly for individuals who struggle with spatial visualization.

# Chapter 6

# General discussion

The four studies presented in this thesis collectively aimed to deepen our understanding of the cognitive and neural mechanisms underlying mental rotation (MR), with a particular focus on how gender, cognitive strategies, testosterone, stimulus types, and individual cognitive traits contribute to MR performance.

Across the experimental studies, I investigated these factors from various perspectives, revealing the complex ways in which top-down cognitive strategies and bottom-up perceptual influences interact to shape MR abilities. In addition, the studies highlighted the role of individual differences in cognitive styles, providing valuable insights into the broader field of spatial cognition. The aims of this thesis were to (1) examine preferences for gender-specific MR strategies; (2) describe the neural correlates of MR and how imagery strategies modulate them; (3) compare brain activations associated with various MR stimuli (abstract, manipulable, and bodily); and (4) evaluate the effects of distinct cognitive traits on brain activity and MR performance.

## Summary of the findings

### *Chapter 2: Cognitive Strategies and Gender Differences*

In Study 1, I investigated the effects of different cognitive strategies on MR performance, particularly in relation to gender differences. I used a novel design aimed at isolating the rotation phase from other cognitive processes. This allowed me to compare performance in three conditions: visuospatial (object-based), motor (effector-based), and a control condition in which no specific strategy was imposed. The results confirmed the well-documented gender differences in MR, with men outperforming women in both the control and object-based conditions. This is consistent with existing literature suggesting that men are more likely to adopt and benefit from spatial strategies, such as the object-based approach, which relies on efficient spatial transformations.

Interestingly, the effector-based condition showed a different pattern, where the gender differences in accuracy decreased. Women showed a significant increase in accuracy when using the effector-based strategy compared to the control condition, suggesting that this strategy may be particularly advantageous for women. This supports previous research suggesting that women may rely more on external landmarks or body-based cues when navigating spatial tasks, as seen in studies of navigation and spatial updating. The results of this study highlight the critical role of cognitive strategies in MR performance and suggest that gender differences may be influenced more by strategic preferences rather than by inherent spatial abilities.

The study also investigated the influence of testosterone on MR performance, but no significant correlations were found between testosterone levels and MR accuracy or reaction times. This challenges the notion that testosterone plays a major role in the observed gender differences in MR, suggesting instead that cognitive strategies and neural processing are more important factors. In addition, the study showed that video game experience, often cited as a factor that could reduce gender differences in spatial tasks, had no significant effect on MR performance in our sample. This highlights the complexity of the factors influencing MR and suggests that the relationship between video game experience and spatial ability may not be as straightforward as previously thought.

### *Chapter 3: Neural Correlates of Strategy and Gender*

Building on the results of Study 1, in Study 2 I used functional magnetic resonance imaging (fMRI) to investigate the neural correlates of MR under different cognitive strategies and to explore how these correlates differ by gender. The results provided further evidence that cognitive strategies are associated with different patterns of brain activation. Specifically, the object-based strategy significantly activated the left pars opercularis, a region implicated in spatial processing and mental rotation. This activation was associated with greater accuracy on the MR tasks, reinforcing the idea that the object-based strategy is an effective spatial approach.

In contrast, the effector-based strategy was associated with activation in motor and sensorimotor cortices, reflecting the motor-oriented nature of this approach. However, despite the activation of these regions, the effector-based strategy was less effective in terms of accuracy, suggesting that the additional cognitive load involved in engaging motor processes might compromise the efficiency of MR. This finding is particularly intriguing as it provides a neural explanation for why motor strategies might be less effective in MR tasks, despite their intuitive appeal.

Gender differences in brain activation were also observed in this study. Women showed additional activation in the somatosensory cortex in the object-based compared to the control condition, which may indicate a reliance on body-based processing. This additional activation could interfere with the deployment of a purely spatial strategy, which may explain why women did not perform as well as men in the object-based condition. These results suggest that gender differences in MR tasks are likely to be influenced by the specific neural strategies employed rather than by inherent differences in spatial abilities.

The study also re-examined the relationship between testosterone and MR performance and found no significant correlations between testosterone levels and brain activity related to MR. This is consistent with the behavioral findings from Study 1 and further challenges the idea that testosterone is a key determinant of sex differences in MR. The lack of a significant relationship between digit ratio (a proxy for prenatal testosterone exposure) and MR performance also suggests that other factors, such as cognitive strategies and neural processing, play a more important role in determining MR ability.

An additional finding from this study was the effect of the order of administration on MR performance. Specifically, performing the effector-based condition first led to improved performance on the subsequent object-based condition for both men and women. This suggests that engaging in a motor, effector-based strategy may serve as a form of training that enhances the effectiveness of a subsequent spatial strategy. This serendipitous finding is particularly interesting as it suggests that the order in which cognitive strategies are used may influence overall MR performance. Future research should further explore this phenomenon to better understand the potential benefits of strategy training in MR tasks.

A notable point between Experiments 1 and 2 is the difference between behavioral performances. Although the design is very similar, we observed a general drop in accuracy. This could be influenced by the position of the participant. In Experiment 1, participants were seated, whereas in Experiment 2, they were lying down inside the MRI scanner. Research suggests that postural differences can impact cognitive performance. Additionally, the MRI environment itself introduces unique challenges due to a reduced attentional focus. These factors likely compounded the performance decline observed in Experiment 2 relative to Experiment 1.

The reduction of the time window in Experiment 2 destined to collect responses could have had an impact as well. For women in particular, previous studies have shown that the error-rate increases in spatial tasks if a time-limit is set.

However, an interesting finding in Experiment 2 is that the performance of male participants remained relatively stable in the object-based strategy (OBS) condition despite the MRI environment, suggesting that OBS may be less susceptible to these environmental and postural challenges. This resilience could indicate that the OBS strategy provides a robust framework for maintaining consistent task engagement under varied conditions, an insight that may inform the design of future experiments aimed at minimizing environmental influences on cognitive task performance.

### *Chapter 4: Impact of Stimulus Type on MR Performance*

Study 3 shifted the focus to the effects of different stimulus types on MR performance and brain activity, and examined how these bottom-up influences interact with gender differences. The study found that stimulus type significantly affected both accuracy and reaction times in MR tasks. Participants performed better when they rotated familiar, manipulable objects than when they rotated more abstract stimuli such as cubes or human body shapes. This finding is consistent with previous research showing that mental images of manipulable objects are easier to generate and manipulate than images of abstract or unfamiliar stimuli.

Gender differences emerged in response to different stimuli, with men showing greater activation in frontal regions, particularly in the superior fronto-medial prefrontal cortex and the right inferior frontal gyrus, when rotating cubes and body figures. This additional activity in prefrontal areas is hypothesized as representing the recruitment of extra spatial processes, as well as the recruitment of holistic, visuo-spatial strategies, that allows them to reach a better performance compared to women.

Women, on the other hand, showed additional activation in the superior parietal lobe and occipital cortex, particularly when the human body pictures were rotated. This pattern of activation suggests that women may rely more on egocentric and visual processing strategies, especially when dealing with stimuli that are more closely related to body-based references.

Interestingly, when accuracy was included as a regressor in the analysis, it was found that increased accuracy in men was associated with increased activation in the precuneus, a region typically associated with spatial strategies. Conversely, decreased accuracy in women was associated with increased activation in motor areas, supporting the idea that motor strategies may interfere with the use of more efficient spatial processes.

The different brain activation patterns observed between men and women for different stimulus categories provide further evidence that gender differences in MR tasks are influenced by the specific neural strategies employed. The study also highlights the importance of considering the type of stimuli used in MR tasks, as different stimuli may engage different neural networks and elicit different cognitive strategies.

### *Chapter 5: Cognitive Traits and Neural Efficiency*

The final study in this thesis examined the role of individual cognitive traits, particularly those related to spatial visualization, perspective taking, and cognitive flexibility, on MR performance and its neural correlates. Using the Object-Spatial Imagery Questionnaire (OSIQ), the perspective-taking test (SOT) and the Cognitive Flexibility Scale (CFS), we investigated how these traits influence MR accuracy and brain activation patterns.

The behavioral results confirmed that participants with higher spatial visualization abilities outperformed those with lower spatial abilities, consistent with the dual coding theory, which suggests that individuals who can efficiently process and manipulate spatial information have a distinct advantage in MR tasks. Perspective taking ability, as measured by the SOT, also showed an influence, with high scorers demonstrating greater accuracy during the MR task. This shows that people who have a good ability to adopt a different perspective in space also perform better when asked to mentally rotate 3D images.

Interestingly, cognitive flexibility, as measured by the Cognitive Flexibility Scale (CFS), did not significantly affect MR performance, challenging the assumption that flexibility in strategy selection is crucial for success in spatial tasks.

The neuroimaging results provided further insight into the neural mechanisms underlying these cognitive traits. Spatial visualizers, who generally performed better on MR tasks, showed more efficient neural processing, with reduced activation in motor and sensorimotor regions. This is consistent with the neural efficiency hypothesis, which proposes that individuals who perform better on cognitive tasks tend to show less brain activation, particularly in regions associated with task-relevant processing. In contrast, object visualizers, who performed worse on MR tasks showed increased activation in these regions, possibly reflecting a compensatory mechanism, or the use of a less efficient cognitive strategy.

A similar result was observed for functional activations in the perspective taking test. Low performers in this task showed greater activation in motor and supplementary motor areas, in the cube vs. body contrast. It seems that when cognitive reorientation proves insufficient, motor strategies can be used to achieve comparable results.

A particularly interesting finding from this study was the observed overlap in activations within the angular gyrus in individuals with lower MR performance. The angular gyrus is a critical region for spatial cognition, particularly in tasks involving visuospatial processing, attention, and the integration of sensory information. The increased activation in this region in lower performers id likely to reflect a compensatory mechanism whereby additional cognitive resources are recruited to cope with the demands of the MR task. However, this increased activation may also indicate less efficient processing, as the brain struggles to perform the necessary spatial transformations.

The overall pattern of results from this study provides strong support for the neural efficiency hypothesis and highlights the role of cognitive styles in determining the efficiency of brain function during spatial tasks. These findings have important implications for understanding the neural and cognitive mechanisms underlying MR performance and suggest that individual differences in cognitive traits play a crucial role in shaping how efficiently the brain processes spatial tasks.

### *Motor Activations and Mental Rotation Performance*

One of the most striking findings across the studies in this thesis is the consistent link between motor and somatosensory activations and lower performance in mental rotation (MR) tasks. This observation provides a deeper understanding of the mechanisms underlying MR performance and challenges the notion that gender differences are the primary explanatory factor.

In all experiments, reliance on motor and somatosensory areas was associated with reduced accuracy. For instance, in Experiment 2, women exhibited increased somatosensory activation during object-based strategies. This activation appears to interfere with the efficiency of spatial processing, which may partly explain the observed differences in performance. Similarly, in Experiment 3, higher activation of the motor cortex was associated with lower accuracy. These findings suggest that motor activations are not inherently tied to gender but rather to the type of strategy employed.

Experiment 4 provided a crucial shift in perspective, demonstrating that individual differences in cognitive traits, such as visuospatial ability, better explain MR performance than gender. Participants with lower visuospatial abilities showed greater reliance on motor and somatosensory regions during MR tasks, which was consistently associated with lower performance. This finding underscores that the neural strategies individuals adopt—whether motor-focused or spatial—are shaped more by their cognitive profiles than by their gender.

Taken together, these results suggest that MR performance is less about inherent gender differences and more about how the brain is used. The adoption of efficient versus inefficient strategies, reflected in the neural activations observed, plays a decisive role in shaping performance outcomes. This insight reframes the discussion from a binary comparison of male versus female performance to a nuanced understanding of individual differences in strategy selection and neural processing.

### *Theoretical Implications*

The results challenge the traditional view that gender differences in MR are purely a result of innate spatial abilities. Instead, they suggest that these differences are the result of the strategies employed during the tasks. For example, men's superior performance in the object-based condition appears to result from their spontaneous use of more effective spatial strategies, whereas women's superior performance in effector-based strategies suggests a reliance on body-based references. These findings suggest that gender differences in MR are likely to be strategic rather than inherent, which has important implications for how we understand and model spatial cognition.

The results also contribute to the ongoing debate about the role of testosterone in spatial abilities. The lack of a significant relationship between testosterone levels and MR performance, both behavioral and neural, suggests that hormonal influences may not be as central to spatial cognition as previously thought. This challenges the notion that testosterone is a primary factor in gender differences in MR, and instead shifts the focus instead to cognitive strategies and neural processing.

The research also extends the neural efficiency hypothesis to the field of MR, showing that individuals with higher spatial visualization abilities have more efficient brain activation patterns. This suggests that cognitive traits, such as spatial visualization, are critical determinants of how efficiently the brain processes spatial tasks. The observed neural differences between spatial and object visualizers provide a deeper understanding of the cognitive and neural strategies underlying MR, and highlight the importance of considering individual differences in cognitive styles in theoretical models of spatial cognition.

### *Practical Implications*

The findings have several practical implications, particularly for educational practice and cognitive training programmes. Given that cognitive strategies play an important role in MR performance, training programmes could be tailored to individual cognitive styles. For example, individuals who naturally rely on motor strategies might benefit from training that gradually introduces more spatially challenging tasks to help them develop more efficient spatial strategies over time.

In addition, the study's findings on stimulus types suggest that the design of MR tasks could be optimized by selecting stimuli that match an individual's cognitive strengths. For example, training with familiar, manipulable objects could serve as a stepping stone to more complex, abstract stimuli, potentially improving overall MR performance.

The research also suggests that gender differences in MR could be mitigated by strategy training. By encouraging the use of effective spatial strategies, such as the object-based approach, women’s performance on MR tasks could be improved, thereby reducing the observed gender gap in spatial cognition. This has important implications for fields that heavily build up on spatial skills, such as STEM (Science, Technology, Engineering, and Mathematics), where women are traditionally underrepresented.

Finally, the accidental finding that performing an effector-based strategy first improves subsequent performance on an object-based task suggests that the order in which tasks are presented may influence learning outcomes. This finding could be used to design more effective training protocols that exploit the benefits of strategy training, potentially improving spatial skills in both educational and occupational contexts.

# Chapter 7

# Conclusion

In summary, this thesis advances our understanding of the cognitive and neural mechanisms underlying MR, particularly in relation to cognitive strategies, stimulus types, gender differences, and individual cognitive traits. The findings suggest that MR performance is influenced by a complex interplay of top-down cognitive strategies and bottom-up perceptual influences, alongside individual differences in cognitive styles.

The research highlights the importance of considering cognitive strategies when studying gender differences in MR, suggesting that these differences are likely to be strategic rather than inherent. Furthermore, the results challenge the traditional view that testosterone is a primary determinant of gender differences in spatial tasks, pointing instead to the critical role of cognitive strategies and neural processing.

My studies also provide strong support for the neural efficiency hypothesis, showing that individuals with higher spatial visualization abilities have more efficient brain activation patterns. This suggests that cognitive traits are crucial determinants of how efficiently the brain processes spatial tasks, with important implications for understanding individual differences in MR performance.

Overall, this dissertation provides a comprehensive picture of the factors that influence MR performance and offers valuable insights for both research and practice. By integrating findings from my four studies, it contributes to a deeper understanding of the cognitive and neural mechanisms underlying MR and provides a solid foundation for future research aimed at enhancing spatial skills and reducing gender differences in spatial cognition.

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## BIBLIOGRAPHY

Abou Khalil, G., Doré-Mazars, K., Senot, P., Wang, D. P., & Legrand, A. (2020). Is it better to sit down, stand up or walk when performing memory and arithmetic activities? *Experimental Brain Research*, *238*(11), 2487–2496. https://doi.org/10.1007/s00221-020-05858-z

Adenzato, M., Brambilla, M., Manenti, R., De Lucia, L., Trojano, L., Garofalo, S., Enrici, I., & Cotelli, M. (2017). Gender differences in cognitive Theory of Mind revealed by transcranial direct current stimulation on medial prefrontal cortex. *Scientific Reports*, *7*(1), 41219. https://doi.org/10.1038/srep41219

Aleman, A., Bronk, E., Kessels, R. P. C., Koppeschaar, H. P. F., & van Honk, J. (2004). A single administration of testosterone improves visuospatial ability in young women. *Psychoneuroendocrinology*, *29*(5), 612–617. https://doi.org/10.1016/S0306-4530(03)00089-1

Alexander, G. M. (2005). *Unpublished data. Correlations between 2D:4D and 3D mental rotation performance.*

Amorim, M.-A., Isableu, B., & Jarraya, M. (2006). Embodied spatial transformations: 'Body analogy' for the mental rotation of objects. *Journal of Experimental Psychology: General*, *135*(3), 327–347. https://doi.org/10.1037/0096-3445.135.3.327

Andersson, J. L. R., Skare, S., & Ashburner, J. (2003). How to correct susceptibility distortions in spin-echo echo-planar images: Application to diffusion tensor imaging. *NeuroImage*, *20*(2), 870–888. https://doi.org/10.1016/S1053-8119(03)00336-7

Arbula, S., Pisanu, E., & Rumiati, R. I. (2021). Representation of social content in dorsomedial prefrontal cortex underlies individual differences in agreeableness trait. *NeuroImage*, *235*, 118049. https://doi.org/10.1016/j.neuroimage.2021.118049

Aso, T., Hanakawa, T., Matsuo, K., Toma, K., Shibasaki, H., Fukuyama, H., & Nakai, T. (2007). Subregions of human parietal cortex selectively encoding object orientation. *Neuroscience Letters*, *415*(3), 225–230. https://doi.org/10.1016/j.neulet.2007.01.051

Assari, S. (2020). Mental Rotation in American Children: Diminished Returns of Parental Education in Black Families. *Pediatric Reports*, *12*(3), 130–141. https://doi.org/10.3390/pediatric12030028

Austin, E., Manning, J., McInroy, K., & Mathews, E. (2002). A preliminary investigation of the associations between personality, cognitive ability and digit ratio. *Personality and Individual Differences*, *33*, 1115–1124. https://doi.org/10.1016/S0191-8869(02)00002-8

Avants, B. B., Epstein, C. L., Grossman, M., & Gee, J. C. (2008). Symmetric diffeomorphic image registration with cross-correlation: Evaluating automated labeling of elderly and neurodegenerative brain. *Medical Image Analysis*, *12*(1), 26–41. https://doi.org/10.1016/j.media.2007.06.004

Baenninger, M., & Newcombe, N. (1989). The role of experience in spatial test performance: A meta-analysis. *Sex Roles*, *20*(5–6), 327–344. https://doi.org/10.1007/BF00287729

Baldo, J. V., & Dronkers, N. F. (2006). The role of inferior parietal and inferior frontal cortex in working memory. *Neuropsychology*, *20*(5), 529–538. https://doi.org/10.1037/0894-4105.20.5.529

Barbey, A., Koenigs, M., & Grafman, J. (2011). Orbitofrontal Contributions to Human Working Memory. *Cerebral Cortex (New York, N.Y.: 1991)*, *21*, 789–795. https://doi.org/10.1093/cercor/bhq153

Barriga, T. (2015). A Meta-analysis of Neuroimaging Studies of Mental Rotation". *Undergraduate Research at FIU (URFIU) Conference*. https://digitalcommons.fiu.edu/fiu-undergraduate-research-conference/2015/posters2015/43

Behzadi, Y., Restom, K., Liau, J., & Liu, T. T. (2007). A component based noise correction method (CompCor) for BOLD and perfusion based fMRI. *NeuroImage*, *37*(1), 90–101. https://doi.org/10.1016/j.neuroimage.2007.04.042

Bell, E. C., Willson, M. C., Wilman, A. H., Dave, S., & Silverstone, P. H. (2006). Males and females differ in brain activation during cognitive tasks. *NeuroImage*, *30*(2), 529–538. https://doi.org/10.1016/j.neuroimage.2005.09.049

Bendall, R. C. A., Galpin, A., Marrow, L. P., & Cassidy, S. (2016). Cognitive Style: Time to Experiment. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01786

Berenbaum, S. A., Bryk, K. L. K., & Beltz, A. M. (2012). Early androgen effects on spatial and mechanical abilities: Evidence from congenital adrenal hyperplasia. *Behavioral Neuroscience*, *126*(1), 86–96. https://doi.org/10.1037/a0026652

Bernal, A., Mateo-Martínez, R., & Paolieri, D. (2020). Influence of sex, menstrual cycle, and hormonal contraceptives on egocentric navigation with or without landmarks. *Psychoneuroendocrinology*, *120*, 104768. https://doi.org/10.1016/j.psyneuen.2020.104768

Bernal, A., & Paolieri, D. (2022). The influence of estradiol and progesterone on neurocognition during three phases of the menstrual cycle: Modulating factors. *Behavioural Brain Research*, *417*, 113593. https://doi.org/10.1016/j.bbr.2021.113593

Bersier, N. M., Arbula, S., Ionta, S., & Rumiati, R. I. (2024). Mental rotation-related neural interactions between gender and cognitive strategy. *Imaging Neuroscience*, *2*, 1–18. https://doi.org/10.1162/imag_a_00310

Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology*, *20*(2), 239–263. https://doi.org/10.1002/acp.1182

Blanke, O., Ionta, S., Fornari, E., Mohr, C., & Maeder, P. (2010). Mental imagery for full and upper human bodies: Common right hemisphere activations and distinct extrastriate activations. *Brain Topography*, *23*(3), 321–332. https://doi.org/10.1007/s10548-010-0138-x

Blanton, R. E., Levitt, J. G., Peterson, J. R., Fadale, D., Sporty, M. L., Lee, M., To, D., Mormino, E. C., Thompson, P. M., McCracken, J. T., & Toga, A. W. (2004). Gender differences in the left inferior frontal gyrus in normal children. *NeuroImage*, *22*(2), 626–636. https://doi.org/10.1016/j.neuroimage.2004.01.010

Boccia, M., Nemmi, F., & Guariglia, C. (2014). Neuropsychology of Environmental Navigation in Humans: Review and Meta-Analysis of fMRI Studies in Healthy Participants. *Neuropsychology Review*, *24*(2), 236–251. https://doi.org/10.1007/s11065-014-9247-8

Bonner, M. F., Peelle, J. E., Cook, P. A., & Grossman, M. (2013). Heteromodal conceptual processing in the angular gyrus. *NeuroImage*, *71*, 175–186. https://doi.org/10.1016/j.neuroimage.2013.01.006

Boone, A., & Hegarty, M. (2015). Strategy differences do not account for gender difference in mental rotation. *Proceedings of the Annual Meeting of the Cognitive Science Society*, *37*.

Boone, A. P., & Hegarty, M. (2017). Sex differences in mental rotation tasks: Not just in the mental rotation process! *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *43*(7), 1005–1019. https://doi.org/10.1037/xlm0000370

Brázdil, M., Mikl, M., Mareček, R., Krupa, P., & Rektor, I. (2007). Effective connectivity in target stimulus processing: A dynamic causal modeling study of visual oddball task. *NeuroImage*, *35*(2), 827–835. https://doi.org/10.1016/j.neuroimage.2006.12.020

Brown, W. M., Hines, M., Fane, B. A., & Breedlove, S. M. (2002). Masculinized finger length patterns in human males and females with congenital adrenal hyperplasia. *Hormones and Behavior*, *42*(4), 380–386. https://doi.org/10.1006/hbeh.2002.1830

Burke, S. M., Kreukels, B. P. C., Cohen-Kettenis, P. T., Veltman, D. J., Klink, D. T., & Bakker, J. (2016). Male-typical visuospatial functioning in gynephilic girls with gender dysphoria—Organizational and activational effects of testosterone. *Journal of Psychiatry & Neuroscience*, *41*(6), 395–404. https://doi.org/10.1503/jpn.150147

Burkitt, J., Widman, D., & Saucier, D. M. (2007). Evidence for the influence of testosterone in the performance of spatial navigation in a virtual water maze in women but not in men. *Hormones and Behavior*, *51*(5), 649–654. https://doi.org/10.1016/j.yhbeh.2007.03.007

Butler, T., Imperato-McGinley, J., Pan, H., Voyer, D., Cordero, J., Zhu, Y.-S., Stern, E., & Silbersweig, D. (2006). Sex differences in mental rotation: Top–down versus bottom–up processing. *NeuroImage*, *32*(1), 445–456. https://doi.org/10.1016/j.neuroimage.2006.03.030

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*(1), 1–47. https://doi.org/10.1162/08989290051137585

Çakır, M. P., Ayaz, H., İzzetoğlu, M., Shewokis, P. A., İzzetoğlu, K., & Onaral, B. (2011). Bridging Brain and Educational Sciences: An Optical Brain Imaging Study of Visuospatial Reasoning. *Procedia - Social and Behavioral Sciences*, *29*, 300–309. https://doi.org/10.1016/j.sbspro.2011.11.243

Calhoun, V. D., Adali, T., McGinty, V. B., Pekar, J. J., Watson, T. D., & Pearlson, G. D. (2001). fMRI Activation in a Visual-Perception Task: Network of Areas Detected

Using the General Linear Model and Independent Components Analysis. *NeuroImage*, *14*(5), 1080–1088. https://doi.org/10.1006/nimg.2001.0921

Campbell, M. J., Toth, A. J., & Brady, N. (2018). Illuminating sex differences in mental rotation using pupillometry. *Biological Psychology*, *138*, 19–26. https://doi.org/10.1016/j.biopsycho.2018.08.003

Castilla, A., Berthoz, A., Urukalo, D., Zaoui, M., Perrochon, A., & Kronovsek, T. (2022). Age and sex impact on visuospatial working memory (VSWM), mental rotation, and cognitive strategies during navigation. *Neuroscience Research*, *183*, 84–96. https://doi.org/10.1016/j.neures.2022.07.007

Ceci, S. J., Williams, W. M., & Barnett, S. M. (2009). Women's underrepresentation in science: Sociocultural and biological considerations. *Psychological Bulletin*, *135*(2), 218–261. https://doi.org/10.1037/a0014412

Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*(10), 913–919. https://doi.org/10.1038/13217

Cherrier, M. M., Asthana, S., Plymate, S., Baker, L., Matsumoto, A. M., Peskind, E., Raskind, M. A., Brodkin, K., Bremner, W., Petrova, A., LaTendresse, S., & Craft, S. (2001). Testosterone supplementation improves spatial and verbal memory in healthy older men. *Neurology*, *57*(1), 80–88. https://doi.org/10.1212/wnl.57.1.80

Cheung, O. S., Hayward, W. G., & Gauthier, I. (2009). Dissociating the effects of angular disparity and image similarity in mental rotation and object recognition. *Cognition*, *113*(1), 128–133. https://doi.org/10.1016/j.cognition.2009.07.008

Christiansen, K., & Knussmann, R. (1987). Sex Hormones and Cognitive Functioning in Men. *Neuropsychobiology*, *18*(1), 27–36. https://doi.org/10.1159/000118389

Christophel, T. B., Cichy, R. M., Hebart, M. N., & Haynes, J.-D. (2015). Parietal and early visual cortices encode working memory content across mental transformations. *NeuroImage*, *106*, 198–206. https://doi.org/10.1016/j.neuroimage.2014.11.018

Christova, P. S., Lewis, S. M., Tagaris, G. A., Uğurbil, K., & Georgopoulos, A. P. (2008). A voxel-by-voxel parametric fMRI study of motor mental rotation: Hemispheric specialization and gender differences in neural processing efficiency. *Experimental Brain Research*, *189*(1), 79–90. https://doi.org/10.1007/s00221-008-1405-x

Clements, D. H., Sarama, J., DiBiase, A. E., & DiBiase, A.-M. (Eds.). (2003). *Engaging Young Children in Mathematics: Standards for Early Childhood Mathematics Education*. Routledge. https://doi.org/10.4324/9781410609236

Cohen, M. S., Kosslyn, S. M., Breiter, H. C., DiGirolamo, G. J., Thompson, W. L., Anderson, A. K., Brookheimer, S. Y., Rosen, B. R., & Belliveau, J. W. (1996). Changes in cortical activity during mental rotation. A mapping study using functional MRI. *Brain: A Journal of Neurology*, *119 ( Pt 1)*, 89–100. https://doi.org/10.1093/brain/119.1.89

Collaer, M. L., & Hines, M. (2020). No Evidence for Enhancement of Spatial Ability with Elevated Prenatal Androgen Exposure in Congenital Adrenal Hyperplasia: A Meta-Analysis. *Archives of Sexual Behavior*, *49*(2), 395–411. https://doi.org/10.1007/s10508-020-01645-7

Connor, J. M., Serbin, L. A., & Schackman, M. (1977). Sex differences in children's response to training on a visual-spatial test. *Developmental Psychology*, *13*(3), 293–294. https://doi.org/10.1037/0012-1649.13.3.293

Coolican, J., & Peters, M. (2003). Sexual dimorphism in the 2D/4D ratio and its relation to mental rotation performance. *Evolution and Human Behavior*, *24*(3), 179–183. https://doi.org/10.1016/S1090-5138(03)00010-2

Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In *Visual information processing* (pp. xiv, 555–xiv, 555). Academic.

Corballis, M. C. (1997). Mental Rotation and the Right Hemisphere. *Brain and Language*, *57*(1), 100–121. https://doi.org/10.1006/brln.1997.1835

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201–215. https://doi.org/10.1038/nrn755

Courvoisier, D. S., Renaud, O., Geiser, C., Paschke, K., Gaudy, K., & Jordan, K. (2013). Sex hormones and mental rotation: An intensive longitudinal investigation. *Hormones and Behavior*, *63*(2), 345–351. https://doi.org/10.1016/j.yhbeh.2012.12.007

Cox, R. W. (1996). AFNI: Software for Analysis and Visualization of Functional Magnetic Resonance Neuroimages. *Computers and Biomedical Research*, *29*(3), 162–173. https://doi.org/10.1006/cbmr.1996.0014

Csatho, A., Karadi, K., & Kallai, J. (2005). *Unpublished data. Correlations between 2D:4D and 3D mental rotation performance.*

Dale, A. M., Fischl, B., & Sereno, M. I. (1999). Cortical Surface-Based Analysis: I. Segmentation and Surface Reconstruction. *NeuroImage*, *9*(2), 179–194. https://doi.org/10.1006/nimg.1998.0395

D'Argembeau, A., Ruby, P., Collette, F., Degueldre, C., Balteau, E., Luxen, A., Maquet, P., & Salmon, E. (2007). Distinct Regions of the Medial Prefrontal Cortex Are Associated with Self-referential Processing and Perspective Taking. *Journal of Cognitive Neuroscience*, *19*(6), 935–944. https://doi.org/10.1162/jocn.2007.19.6.935

Dawson, J. L., Cheung, Y. M., & Lau, R. T. (1975). Developmental effects of neonatal sex hormones on spatial and activity skills in the white rat. *Biological Psychology*, *3*(3). https://doi.org/10.1016/0301-0511(75)90036-8

de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage*, *33*(2), 609–617. https://doi.org/10.1016/j.neuroimage.2006.07.017

De Lisi, R., & Wolford, J. L. (2002). Improving Children's Mental Rotation Accuracy With Computer Game Playing. *The Journal of Genetic Psychology*, *163*(3), 272–282. https://doi.org/10.1080/00221320209598683

Doganci, N., Yahia Coll, S., Marti, E., & Ptak, R. (2024). Anatomical predictors of mental rotation with bodily and non-bodily stimuli: A lesion-symptom study. *Neuropsychologia*, *193*, 108775. https://doi.org/10.1016/j.neuropsychologia.2023.108775

Doyle, R. A., & Voyer, D. (2013). Bodies and occlusion: Item types, cognitive processes, and gender differences in mental rotation. *Quarterly Journal of Experimental Psychology*, *66*(4), 801–815. https://doi.org/10.1080/17470218.2012.719529

Doyle, R. A., & Voyer, D. (2018). Photographs of real human figures: Item types and persistent sex differences in mental rotation. *Quarterly Journal of Experimental Psychology*, *71*(11), 2411–2420.

Doyle, R. A., Voyer, D., & Lesmana, M. (2016). Item type, occlusion, and gender differences in mental rotation. *Quarterly Journal of Experimental Psychology*, *69*(8), 1530–1544. https://doi.org/10.1080/17470218.2015.1086807

Ehrsson, H. H., Geyer, S., & Naito, E. (2003). Imagery of Voluntary Movement of Fingers, Toes, and Tongue Activates Corresponding Body-Part-Specific Motor Representations. *Journal of Neurophysiology*, *90*(5), 3304–3316. https://doi.org/10.1152/jn.01113.2002

Esteban, O., Birman, D., Schaer, M., Koyejo, O. O., Poldrack, R. A., & Gorgolewski, K. J. (2017). MRIQC: Advancing the automatic prediction of image quality in MRI from unseen sites. *PLOS ONE*, *12*(9), e0184661. https://doi.org/10.1371/journal.pone.0184661

Esteban, O., Blair, R. W., Nielson, D. M., Varada, J. C., Marrett, S., Thomas, A. G., Poldrack, R. A., & Gorgolewski, K. J. (2019). Crowdsourced MRI quality metrics and expert quality annotations for training of humans and machines. *Scientific Data*, *6*(1), 30. https://doi.org/10.1038/s41597-019-0035-4

Esteban, O., Markiewicz, C. J., Blair, R. W., Moodie, C. A., Isik, A. I., Erramuzpe, A., Kent, J. D., Goncalves, M., DuPre, E., Snyder, M., Oya, H., Ghosh, S. S., Wright, J., Durnez, J., Poldrack, R. A., & Gorgolewski, K. J. (2019). fMRIPrep: A robust preprocessing pipeline for functional MRI. *Nature Methods*, *16*(1), Article 1. https://doi.org/10.1038/s41592-018-0235-4

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*(2), 175–191. https://doi.org/10.3758/bf03193146

Feng, J., Spence, I., & Pratt, J. (2007). Playing an Action Video Game Reduces Gender Differences in Spatial Cognition. *Psychological Science*, *18*, 850–855. https://doi.org/10.1111/j.1467-9280.2007.01990.x

Ferguson, T. D., Livingstone-Lee, S. A., & Skelton, R. W. (2019). Incidental learning of allocentric and egocentric strategies by both men and women in a dual-strategy virtual Morris water maze. *Behavioural Brain Research*, *364*, 281–295. https://doi.org/10.1016/j.bbr.2019.02.032

Fisher, M. L., Meredith, T., & Gray, M. (2018). Sex Differences in Mental Rotation Ability Are a Consequence of Procedure and Artificiality of Stimuli. *Evolutionary Psychological Science*, *4*(2), 124–133. https://doi.org/10.1007/s40806-017-0120-x

Fonov, V. S., Evans, A. C., McKinstry, R. C., Almli, C. R., & Collins, D. L. (2009). Unbiased nonlinear average age-appropriate brain templates from birth to adulthood. *NeuroImage*, *54*(1), 313–327. https://doi.org/10.1016/S1053-8119(09)70884-5

Frick, A., Möhring, W., & Newcombe, N. S. (2014). Development of mental transformation abilities. *Trends in Cognitive Sciences*, *18*(10), 536–542. https://doi.org/10.1016/j.tics.2014.05.011

Frith, C. d., Wolpert, D. m., Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *358*(1431), 459–473. https://doi.org/10.1098/rstb.2002.1218

Funk, M., & Brugger, P. (2008). Mental rotation of congenitally absent hands. *Journal of the International Neuropsychological Society*, *14*(1), 81–89. https://doi.org/10.1017/S1355617708080041

Geary, D. C. (1995). Sexual selection and sex differences in spatial cognition. *Learning and Individual Differences*, *7*(4), 289–301. https://doi.org/10.1016/1041-6080(95)90003-9

Geary, D. C. (1998). *Male, female: The evolution of human sex differences* (pp. xii, 397). American Psychological Association. https://doi.org/10.1037/10370-000

Geisen, M., Raab, M., Jansen, P., & Klatt, S. (2024). Embodied mental rotation ability in open- and closed-skill sports: Pilot study with a new virtual paradigm. *Experimental Brain Research*, *242*(3), 653–664. https://doi.org/10.1007/s00221-023-06753-z

Geva, D., & Henik, A. (2019). Perspective taking in judgment of relative direction tasks. *Memory & Cognition*, *47*(6), 1215–1230. https://doi.org/10.3758/s13421-019-00929-1

Giovaola, Y., Rojo Martinez, V., & Ionta, S. (2022). Degraded vision affects mental representations of the body. *Visual Cognition*, *30*(10), 686–695. https://doi.org/10.1080/13506285.2023.2186997

Gordon, H. W., & Lee, P. A. (1993). No difference in cognitive performance between phases of the menstrual cycle. *Psychoneuroendocrinology*, *18*(7), 521–531. https://doi.org/10.1016/0306-4530(93)90045-m

Gorgolewski, K., Burns, C., Madison, C., Clark, D., Halchenko, Y., Waskom, M., & Ghosh, S. (2011). Nipype: A Flexible, Lightweight and Extensible Neuroimaging Data Processing Framework in Python. *Frontiers in Neuroinformatics*, *5*. https://www.frontiersin.org/articles/10.3389/fninf.2011.00013

Greve, D., N., & Fischl, B. (2009). *Accurate and robust brain image alignment using boundary-based registration*. *48*(1), 63–72.

Grèzes, J., Tucker, M., Armony, J., Ellis, R., & Passingham, R. E. (2003). Objects automatically potentiate action: An fMRI study of implicit processing. *The European Journal of Neuroscience*, *17*(12), 2735–2740. https://doi.org/10.1046/j.1460-9568.2003.02695.x

Griksiene, R., Arnatkeviciute, A., Monciunskaite, R., Koenig, T., & Ruksenas, O. (2019). Mental rotation of sequentially presented 3D figures: Sex and sex hormones related differences in behavioural and ERP measures. *Scientific Reports*, *9*(1), Article 1. https://doi.org/10.1038/s41598-019-55433-y

Guizzo, F., Moè, A., Cadinu, M., & Bertolli, C. (2019). The role of implicit gender spatial stereotyping in mental rotation performance. *Acta Psychologica*, *194*, 63–68. https://doi.org/10.1016/j.actpsy.2019.01.013

Gurvich, C., Nicholls, I., Lavale, A., & Kulkarni, J. (2023). Oral contraceptives and cognition: A systematic review. *Frontiers in Neuroendocrinology*, *69*, 101052. https://doi.org/10.1016/j.yfrne.2022.101052

Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences*, *98*(7), 4259–4264. https://doi.org/10.1073/pnas.071043098

Haciomeroglu, E. S., & LaVenia, M. (2017). Object-Spatial Imagery and Verbal Cognitive Styles in High School Students. *Perceptual and Motor Skills*, *124*(3), 689–702. https://doi.org/10.1177/0031512517698555

Haier, R. J., Siegel, B., Tang, C., Abel, L., & Buchsbaum, M. S. (1992). Intelligence and changes in regional cerebral glucose metabolic rate following learning. *Intelligence*, *16*(3), 415–426. https://doi.org/10.1016/0160-2896(92)90018-M

Halpern, D. F. (2013). *Sex Differences in Cognitive Abilities: 4th Edition*. Psychology Press.

Hammers, A., Chen, C.-H., Lemieux, L., Allom, R., Vossos, S., Free, S. L., Myers, R., Brooks, D. J., Duncan, J. S., & Koepp, M. J. (2007). Statistical neuroanatomy of the human inferior frontal gyrus and probabilistic atlas in a standard stereotaxic space. *Human Brain Mapping*, *28*(1), 34–48. https://doi.org/10.1002/hbm.20254

Hampson, E., Rovet, J. F., & Altmann, D. (1998). Spatial reasoning in children with congenital adrenal hyperplasia due to 21-hydroxylase deficiency. *Developmental Neuropsychology*, *14*(2–3), 299–320. https://doi.org/10.1080/87565649809540713

Harasty, J., Double, K. L., Halliday, G. M., Kril, J. J., & McRitchie, D. A. (1997). Language-Associated Cortical Regions Are Proportionally Larger in the Female Brain. *Archives of Neurology*, *54*(2), 171–176. https://doi.org/10.1001/archneur.1997.00550140045011

Harris, I. M., & Miniussi, C. (2003). Parietal Lobe Contribution to Mental Rotation Demonstrated with rTMS. *Journal of Cognitive Neuroscience*, *15*(3), 315–323. https://doi.org/10.1162/089892903321593054

Hassler, M., Gupta, D., & Wollmann, H. (1992). Testosterone, Estradiol, Acth and Musical, Spatial and Verbal Performance. *International Journal of Neuroscience*, *65*(1–4), 45–60. https://doi.org/10.3109/00207459209003277

Hausmann, M., Slabbekoorn, D., Van Goozen, S. H., Cohen-Kettenis, P. T., & Güntürkün, O. (2000). Sex hormones affect spatial abilities during the menstrual cycle. *Behavioral Neuroscience*, *114*(6), 1245–1250. https://doi.org/10.1037//0735-7044.114.6.1245

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science (New York, N.Y.)*, *293*(5539), 2425–2430. https://doi.org/10.1126/science.1063736

Hegarty, M. (2018). Ability and sex differences in spatial thinking: What does the mental rotation test really measure? *Psychonomic Bulletin & Review*, *25*(3), 1212–1219. https://doi.org/10.3758/s13423-017-1347-z

Hegarty, M., & Waller, D. (2004). A dissociation between mental rotation and perspective-taking spatial abilities. *Intelligence*, *32*(2), 175–191. https://doi.org/10.1016/j.intell.2003.12.001

Helleday, J., Bartfai, A., Ritzén, E., & Forsman, M. (1994). General intelligence and cognitive profile in women with congenital adrenal hyperplasia (CAH). *Psychoneuroendocrinology*, *19*(4). https://doi.org/10.1016/0306-4530(94)90015-9

Herath, P., Kinomura, S., & Roland, P. E. (2001). Visual recognition: Evidence for two distinctive mechanisms from a PET study. *Human Brain Mapping*, *12*(2), 110–119. https://doi.org/10.1002/1097-0193(200102)12:2<110::aid-hbm1008>3.0.co;2-0

Hertanti, A., Retnawati, H., & Wutsqa, D. U. (2019). The role of spatial experience in mental rotation. *Journal of Physics: Conference Series*, *1320*(1), 012043. https://doi.org/10.1088/1742-6596/1320/1/012043

Hines, M., Fane, B. A., Pasterski, V. L., Mathews, G. A., Conway, G. S., & Brook, C. (2003). Spatial abilities following prenatal androgen abnormality: Targeting and mental rotations performance in individuals with congenital adrenal hyperplasia. *Psychoneuroendocrinology*, *28*(8), 1010–1026. https://doi.org/10.1016/s0306-4530(02)00121-x

Hirai, M., Sakurada, T., Ikeda, T., Monden, Y., Shimoizumi, H., & Yamagata, T. (2022). Developmental changes of the neural mechanisms underlying level 2 visual perspective-taking: A functional near-infrared spectroscopy study. *Developmental Psychobiology*, *64*(1), e22229. https://doi.org/10.1002/dev.22229

Hooven, C. K., Chabris, C. F., Ellison, P. T., & Kosslyn, S. M. (2004). The relationship of male testosterone to components of mental rotation. *Neuropsychologia*, *42*(6), 782–790. https://doi.org/10.1016/j.neuropsychologia.2003.11.012

Hromatko, I., & Tadinac, M. (2006). Testosterone levels influence spatial ability: Further evidence for curvilinear relationship. *Annual Review of Psychology*. https://www.semanticscholar.org/paper/Testosterone-levels-influence-spatial-ability%3A-for-Hromatko-Tadinac/1a60590d992dff63c99e4b316271f572085da4ed

Hugdahl, K., Thomsen, T., & Ersland, L. (2006). Sex differences in visuo-spatial processing: An fMRI study of mental rotation. *Neuropsychologia*, *44*(9), 1575–1583. https://doi.org/10.1016/j.neuropsychologia.2006.01.026

Hughes, I. A., Davies, J. D., Bunch, T. I., Pasterski, V., Mastroyannopoulou, K., & MacDougall, J. (2012). Androgen insensitivity syndrome. *The Lancet*, *380*(9851), 1419–1428. https://doi.org/10.1016/S0140-6736(12)60071-3

Hyun, J.-S., & Luck, S. J. (2007). Visual working memory as the substrate for mental rotation. *Psychonomic Bulletin & Review*, *14*(1), 154–158. https://doi.org/10.3758/BF03194043

Iachini, T., Ruggiero, G., Bartolo, A., Rapuano, M., & Ruotolo, F. (2019). The Effect of Body-Related Stimuli on Mental Rotation in Children, Young and Elderly Adults. *Scientific Reports*, *9*(1), 1169. https://doi.org/10.1038/s41598-018-37729-7

Ionescu, T. (2012). Exploring the nature of cognitive flexibility. *New Ideas in Psychology*, *30*(2), 190–200. https://doi.org/10.1016/j.newideapsych.2011.11.001

Ionta, S., Fourkas, A. D., & Aglioti, S. M. (2010). Egocentric and object-based transformations in the laterality judgement of human and animal faces and of non-corporeal objects. *Behavioural Brain Research*, *207*(2), 452–457. https://doi.org/10.1016/j.bbr.2009.10.037

Ionta, S., Sforza, A., Funato, M., & Blanke, O. (2013). Anatomically plausible illusory posture affects mental rotation of body parts. *Cognitive, Affective, & Behavioral Neuroscience*, *13*(1), 197–209. https://doi.org/10.3758/s13415-012-0120-z

Isgor, C., & Sengelaub, D. R. (1998). Prenatal gonadal steroids affect adult spatial behavior, CA1 and CA3 pyramidal cell morphology in rats. *Hormones and Behavior*, *34*(2), 183–198. https://doi.org/10.1006/hbeh.1998.1477

Isgor, C., & Sengelaub, D. R. (2003). Effects of neonatal gonadal steroids on adult CA3 pyramidal neuron dendritic morphology and spatial memory in rats. *Journal of Neurobiology*, *55*(2), 179–190. https://doi.org/10.1002/neu.10200

Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences of the United States of America*, *96*(16), 9379–9384. https://doi.org/10.1073/pnas.96.16.9379

Janowsky, J. S. (2006). Thinking with your gonads: Testosterone and cognition. *Trends in Cognitive Sciences*, *10*(2), 77–82. https://doi.org/10.1016/j.tics.2005.12.010

Jansen, P., Paes, F., Hoja, S., & Machado, S. (2019). Mental Rotation Test Performance in Brazilian and German Adolescents: The Role of Sex, Processing Speed, and Physical Activity in Two Different Cultures. *Frontiers in Psychology*, *10*, 945. https://doi.org/10.3389/fpsyg.2019.00945

Jansen, P., & Pietsch, S. (2010). Physical Activity Improves Mental Rotation Performance. *Creative Education*, *01*(01), 58–61. https://doi.org/10.4236/ce.2010.11009

Jansen, P., Render, A., Scheer, C., & Siebertz, M. (2020). Mental rotation with abstract and embodied objects as stimuli: Evidence from event-related potential (ERP). *Experimental Brain Research*, *238*(3), 525–535. https://doi.org/10.1007/s00221-020-05734-w

Jansen-Osmann, P., & Heil, M. (2007). Suitable stimuli to obtain (no) gender differences in the speed of cognitive processes involved in mental rotation. *Brain and Cognition*, *64*(3), 217–227. https://doi.org/10.1016/j.bandc.2007.03.002

Janssen, A. B., & Geiser, C. (2012). Cross-Cultural Differences in Spatial Abilities and Solution Strategies—An Investigation in Cambodia and Germany. *Journal of Cross-Cultural Psychology*, *43*(4), 533–557. https://doi.org/10.1177/0022022111399646

Jenkinson, M., Bannister, P., Brady, M., & Smith, S. (2002). Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. *NeuroImage*, *17*(2), 825–841. https://doi.org/10.1006/nimg.2002.1132

Jiménez, J. A., Mancini-Marïe, A., Lakis, N., Rinaldi, M., & Mendrek, A. (2010). Disturbed sexual dimorphism of brain activation during mental rotation in schizophrenia. *Schizophrenia Research*, *122*(1–3), 53–62. https://doi.org/10.1016/j.schres.2010.03.011

Johnson, S. P., & Moore, D. S. (2020). Spatial thinking in infancy: Origins and development of mental rotation between 3 and 10 months of age. *Cognitive Research: Principles and Implications*, *5*(1), 10. https://doi.org/10.1186/s41235-020-00212-x

Johnston, S., Leek, E. C., Atherton, C., Thacker, N., & Jackson, A. (2004). Functional contribution of medial premotor cortex to visuo-spatial transformation in humans. *Neuroscience Letters*, *355*(3), 209–212. https://doi.org/10.1016/j.neulet.2003.11.011

Jonassen, D., & Grabowski, B. (1993). *Handbook of Individual Differences, Learning, and Instruction | David.* https://www.taylorfrancis.com/books/mono/10.4324/9780203052860/handbook-individual-differences-learning-instruction-david-jonassen-barbara-grabowski

Jordan, K. (2002). Women and men exhibit different cortical activation patterns during mental rotation tasks. *Neuropsychologia*, *40*(13), 2397–2408. https://doi.org/10.1016/S0028-3932(02)00076-3

Jordan, K., Wüstenberg, T., Heinze, H-J, Peters, M., & Jäncke, L. (2002). Women and men exhibit different cortical activation patterns during mental rotation tasks. *Neuropsychologia*, *40*, 2397–2408. https://doi.org/10.1016/S0028-3932(02)00076-3

Joseph, R., Hess, S., & Birecree, E. (1978). Effects of hormone manipulations and exploration on sex differences in maze learning. *Behavioral Biology*, *24*(3), 364–377. https://doi.org/10.1016/s0091-6773(79)90223-2

Jost, L., & Jansen, P. (2023). The influence of the design of mental rotation trials on performance and possible differences between sexes: A theoretical review and experimental investigation. *Quarterly Journal of Experimental Psychology*, 17470218231200127. https://doi.org/10.1177/17470218231200127

Kaiser, S., Walther, S., Nennig, E., Kronmüller, K., Mundt, C., Weisbrod, M., Stippich, C., & Vogeley, K. (2008). Gender-specific strategy use and neural correlates in a spatial perspective taking task. *Neuropsychologia*, *46*(10), 2524–2531. https://doi.org/10.1016/j.neuropsychologia.2008.04.013

Kempel, P., Burk, C., & Hennig, J. (2005). *Unpublished data. Correlations between 2D:4D and 3D mental rotation performance.*

Kempel, P., Gohlke, B., Klempau, J., Zinsberger, P., Reuter, M., & Hennig, J. (2005). Second-to-fourth digit length, testosterone and spatial ability. *Intelligence*, *33*(3), 215–230. https://doi.org/10.1016/j.intell.2004.11.004

Kim, W., Chang, Y., Kim, J., Seo, J., Ryu, K., Lee, E., Woo, M., & Janelle, C. M. (2014). An fMRI study of differences in brain activity among elite, expert, and novice archers at the moment of optimal aiming. *Cognitive and Behavioral Neurology: Official Journal of the Society for Behavioral and Cognitive Neurology*, *27*(4), 173–182. https://doi.org/10.1097/WNN.0000000000000042

Klein, A., Ghosh, S. S., Bao, F. S., Giard, J., Häme, Y., Stavsky, E., Lee, N., Rossa, B., Reuter, M., Neto, E. C., & Keshavan, A. (2017). Mindboggling morphometry of human brains. *PLOS Computational Biology*, *13*(2), e1005350. https://doi.org/10.1371/journal.pcbi.1005350

Klein, G. S. (1951). The personal world through perception. In *Perception: An approach to personality* (pp. 328–355). Ronald Press Company. https://doi.org/10.1037/11505-012

Koriat, A., & Norman, J. (1985). Mental rotation and visual familiarity. *Perception & Psychophysics*, *37*(5), 429–439. https://doi.org/10.3758/BF03202874

Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: Neural mechanisms revealed by positron emission tomography. *Psychophysiology*, *35*(2), 151–161.

Kozhevnikov, M. (2007). Cognitive styles in the context of modern psychology: Toward an integrated framework of cognitive style. *Psychological Bulletin*, *133*(3), 464–481. https://doi.org/10.1037/0033-2909.133.3.464

Kozhevnikov, M., & Hegarty, M. (2001). A dissociation between object manipulation spatial ability and spatial orientation ability. *Memory & Cognition*, *29*(5), 745–756. https://doi.org/10.3758/BF03200477

Kozhevnikov, M., Hegarty, M., & Mayer, R. E. (2002). Revising the Visualizer-Verbalizer Dimension: Evidence for Two Types of Visualizers. *Cognition and Instruction*, *20*(1), 47–77. https://doi.org/10.1207/S1532690XCI2001_3

Kozhevnikov, M., Kosslyn, S., & Shephard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory & Cognition*, *33*(4), 710–726. https://doi.org/10.3758/BF03195337

Kozhevnikov, M., Kozhevnikov, M., Yu, C. J., & Blazhenkova, O. (2013). Creativity, visualization abilities, and visual cognitive style. *British Journal of Educational Psychology*, *83*(2), 196–209. https://doi.org/10.1111/bjep.12013

Kozhevnikov, M., Motes, M. A., Rasch, B., & Blajenkova, O. (2006). Perspective-taking vs. Mental rotation transformations and how they predict spatial navigation performance. *Applied Cognitive Psychology*, *20*(3), 397–417. https://doi.org/10.1002/acp.1192

Krüger, M., Amorim, M.-A., & Ebersbach, M. (2014). Mental rotation and the motor system: Embodiment head over heels. *Acta Psychologica*, *145*, 104–110. https://doi.org/10.1016/j.actpsy.2013.11.004

Kubranská, A., Lakatošová, S., Schmidtová, E., Durdiaková, J., Celec, P., & Ostatníková, D. (2014). Spatial abilities are not related to testosterone levels and variation in the androgen receptor in healthy young men. *General Physiology and Biophysics*, *33*(03), 311–319. https://doi.org/10.4149/gpb_2014005

Lambrey, S., & Berthoz, A. (2007). Gender differences in the use of external landmarks versus spatial representations updated by self-motion. *Journal of Integrative Neuroscience, 06*(03), 379–401. https://doi.org/10.1142/S021963520700157X

Lambrey, S., Doeller, C., Berthoz, A., & Burgess, N. (2012). Imagining Being Somewhere Else: Neural Basis of Changing Perspective in Space. *Cerebral Cortex*, *22*(1), 166–174. https://doi.org/10.1093/cercor/bhr101

Lamm, C., Windischberger, C., Moser, E., & Bauer, H. (2007). The functional role of dorso-lateral premotor cortex during mental rotation: An event-related fMRI study separating cognitive processing steps using a novel task paradigm. *NeuroImage*, *36*(4), 1374–1386. https://doi.org/10.1016/j.neuroimage.2007.04.012

Lehmann, J., & Jansen, P. (2019). The relationship between theory of mind and mental rotation ability in preschool-aged children. *Cogent Psychology*, *6*(1), 1582127. https://doi.org/10.1080/23311908.2019.1582127

Lehmann, J., Quaiser-Pohl, C., & Jansen, P. (2014). Correlation of motor skill, mental rotation, and working memory in 3- to 6-year-old children. *European Journal of Developmental Psychology*, *11*(5), 560–573. https://doi.org/10.1080/17405629.2014.888995

Lev-Ran, S., Shamay-Tsoory, S. G., Zangen, A., & Levkovitz, Y. (2012). Transcranial magnetic stimulation of the ventromedial prefrontal cortex impairs theory of mind learning. *European Psychiatry*, *27*(4), 285–289. https://doi.org/10.1016/j.eurpsy.2010.11.008

Linn, M. C., & Petersen, A. C. (1985). Emergence and Characterization of Sex Differences in Spatial Ability: A Meta-Analysis. *Child Development*, *56*(6), 1479–1498. https://doi.org/10.2307/1130467

Loehlin, J. C., Luciano, M., Medland, S. E., & Martin, N. G. (2005). *Unpublished data. Correlations between 2D:4D and 3D mental rotation performance.*

Long, H., Fan, M., Yang, X., Guan, Q., Huang, Y., Xu, X., Xiao, J., & Jiang, T. (2021). Sex-related Difference in Mental Rotation Performance is Mediated by the special Functional Connectivity Between the Default Mode and Salience Networks. *Neuroscience*, *478*, 65–74. https://doi.org/10.1016/j.neuroscience.2021.10.009

Longo, M. R., & Haggard, P. (2010). An implicit body representation underlying human position sense. *Proceedings of the National Academy of Sciences*, *107*(26), 11727–11732. https://doi.org/10.1073/pnas.1003483107

Malouf, M. A., Migeon, C. J., Carson, K. A., Petrucci, L., & Wisniewski, A. B. (2006). Cognitive outcome in adult women affected by congenital adrenal hyperplasia due to 21-hydroxylase deficiency. *Hormone Research*, *65*(3), 142–150. https://doi.org/10.1159/000091793

Manning, J., & Fink, B. (2018). Digit Ratio. *Encyclopedia of Evolutionary Psychological Science*, 1–12. https://doi.org/10.1007/978-3-319-16999-6_3829-1

Manning, J. T., Scutt, D., Wilson, J., & Lewis-Jones, D. I. (1998). The ratio of 2nd to 4th digit length: A predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Human Reproduction (Oxford, England)*, *13*(11), 3000–3004. https://doi.org/10.1093/humrep/13.11.3000

Manning, J. T., & Taylor, R. P. (2001). Second to fourth digit ratio and male ability in sport: Implications for sexual selection in humans. *Evolution and Human Behavior: Official Journal of the Human Behavior and Evolution Society*, *22*(1), 61–69. https://doi.org/10.1016/s1090-5138(00)00063-5

Maravita, A., & Iriki, A. (2004). Tools for the body (schema). *Trends in Cognitive Sciences*, *8*(2), 79–86. https://doi.org/10.1016/j.tics.2003.12.008

Marois, R., & Ivanoff, J. (2005). Capacity limits of information processing in the brain. *Trends in Cognitive Sciences*, *9*(6), 296–305. https://doi.org/10.1016/j.tics.2005.04.010

Marques, J. P., Kober, T., Krueger, G., van der Zwaag, W., Van de Moortele, P.-F., & Gruetter, R. (2010). MP2RAGE, a self bias-field corrected sequence for improved segmentation and T1-mapping at high field. *NeuroImage*, *49*(2), 1271–1281. https://doi.org/10.1016/j.neuroimage.2009.10.002

Martin, M. M., & Rubin, R. B. (1995). A New Measure of Cognitive Flexibility. *Psychological Reports*, *76*(2), 623–626. https://doi.org/10.2466/pr0.1995.76.2.623

Martinez, V. R., Giovanola, Y., & Ionta, S. (2022). Social Touch Somatotopically Affects Mental Body Representations. *Neuroscience*, *494*, 178–186. https://doi.org/10.1016/j.neuroscience.2022.05.017

Mayer, R. E., & Massa, L. J. (2003). Three Facets of Visual and Verbal Learners: Cognitive Ability, Cognitive Style, and Learning Preference. *Journal of Educational Psychology*, *95*(4), 833–846. https://doi.org/10.1037/0022-0663.95.4.833

McFadden, D., & Shubel, E. (2003). The relationships between otoacoustic emissions and relative lengths of fingers and toes in humans. *Hormones and Behavior*, *43*(3), 421–429. https://doi.org/10.1016/s0018-506x(03)00014-x

McGuire, L. S., Ryan, K. O., & Omenn, G. S. (1975). Congenital adrenal hyperplasia. II. Cognitive and behavioral studies. *Behavior Genetics*, *5*(2), 175–188. https://doi.org/10.1007/BF01066810

Mendrek, A., Lakis, N., & Jiménez, J. (2011). Associations of sex steroid hormones with cerebral activations during mental rotation in men and women with schizophrenia. *Psychoneuroendocrinology*, *36*(9), 1422–1426. https://doi.org/10.1016/j.psyneuen.2011.03.016

Menéndez Granda, M., Iannotti, G. R., Darqué, A., & Ptak, R. (2022). Does mental rotation emulate motor processes? An electrophysiological study of objects and body parts. *Frontiers in Human Neuroscience*, *16*, 983137. https://doi.org/10.3389/fnhum.2022.983137

Menon, V., & Uddin, L. Q. (2010). Saliency, switching, attention and control: A network model of insula function. *Brain Structure and Function*, *214*(5), 655–667. https://doi.org/10.1007/s00429-010-0262-0

Mesulam, M. M. (1998). From sensation to cognition. *Brain: A Journal of Neurology*, *121 (Pt 6)*, 1013–1052. https://doi.org/10.1093/brain/121.6.1013

Miller, D. I., & Halpern, D. F. (2014). The new science of cognitive sex differences. *Trends in Cognitive Sciences*, *18*(1), 37–45. https://doi.org/10.1016/j.tics.2013.10.011

Minamoto, T., Osaka, M., & Osaka, N. (2010). Individual differences in working memory capacity and distractor processing: Possible contribution of top–down inhibitory control. *Brain Research*, *1335*, 63–73. https://doi.org/10.1016/j.brainres.2010.03.088

Mitchel, J. P., Macrae, N. C., & Banaji, M. R. (2005). The Link between Social Cognition and Self-referential Thought in the Medial Prefrontal Cortex. *Journal of Cognitive Neuroscience*, *17*(8), 1306–1315.

Moè, A., Hausmann, M., & Hirnstein, M. (2021). Gender stereotypes and incremental beliefs in STEM and non-STEM students in three countries: Relationships with performance in cognitive tasks. *Psychological Research*, *85*(2), 554–567. https://doi.org/10.1007/s00426-019-01285-0

Moffat, S., & Hampson, E. (1996). A curvilinear relationship between testosterone and spatial cognition in humans: Possible influence of hand preference. *Psychoneuroendocrinology*, *21*(3), 323–337. https://doi.org/10.1016/0306-4530(95)00051-8

Moore, D. S., & Johnson, S. P. (2020). The development of mental rotation ability across the first year after birth. *Advances in Child Development and Behavior*, *58*, 1–33. https://doi.org/10.1016/bs.acdb.2020.01.001

Motes, M. A., Malach, R., & Kozhevnikov, M. (2008). Object-processing neural efficiency differentiates object from spatial visualizers. *NeuroReport*, *19*(17), 1727. https://doi.org/10.1097/WNR.0b013e328317f3e2

Mueller, S. C., Temple, V., Oh, E., VanRyzin, C., Williams, A., Cornwell, B., Grillon, C., Pine, D. S., Ernst, M., & Merke, D. (2008). Early androgen exposure modulates spatial cognition in congenital adrenal hyperplasia (CAH). *Psychoneuroendocrinology*, *33*(7), 973–980. https://doi.org/10.1016/j.psyneuen.2008.04.005

Mutlu, M. C., Erdoğan, S. B., Öztürk, O. C., Canbeyli, R., & Saybaşılı, H. (2020). Functional Near-Infrared Spectroscopy Indicates That Asymmetric Right Hemispheric Activation in Mental Rotation of a Jigsaw Puzzle Decreases With Task Difficulty. *Frontiers in Human Neuroscience*, *14*, 252. https://doi.org/10.3389/fnhum.2020.00252

Muto, H. (2021). Correlational Evidence for the Role of Spatial Perspective-Taking Ability in the Mental Rotation of Human-Like Objects. *Experimental Psychology*, *68*(1), 41–48. https://doi.org/10.1027/1618-3169/a000505

Naito, E., & Ehrsson, H. H. (2006). Somatic Sensation of Hand-Object Interactive Movement Is Associated with Activity in the Left Inferior Parietal Cortex. *Journal of Neuroscience*, *26*(14), 3783–3790. https://doi.org/10.1523/JNEUROSCI.4835-05.2006

Naito, E., Ehrsson, H. H., Geyer, S., Zilles, K., & Roland, P. E. (1999). Illusory Arm Movements Activate Cortical Motor Areas: A Positron Emission Tomography Study. *Journal of Neuroscience*, *19*(14), 6134–6144. https://doi.org/10.1523/JNEUROSCI.19-14-06134.1999

Naito, E., Morita, T., & Amemiya, K. (2016). Body representations in the human brain revealed by kinesthetic illusions and their essential contributions to motor control and corporeal awareness. *Neuroscience Research*, *104*, 16–30. https://doi.org/10.1016/j.neures.2015.10.013

Naito, E., Roland, P. E., & Ehrsson, H. H. (2002). I Feel My Hand Moving: A New Role of the Primary Motor Cortex in Somatic Perception of Limb Movement. *Neuron*, *36*(5), 979–988. https://doi.org/10.1016/S0896-6273(02)00980-7

Nazareth, A., Herrera, A., & Pruden, S. M. (2013). Explaining sex differences in mental rotation: Role of spatial activity experience. *Cognitive Processing*, *14*(2), 201–204. https://doi.org/10.1007/s10339-013-0542-8

Nazareth, A., Killick, R., Dick, A. S., & Pruden, S. M. (2019). Strategy selection versus flexibility: Using eye-trackers to investigate strategy use during mental rotation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *45*(2), 232–245. https://doi.org/10.1037/xlm0000574

Nixon, P., Lazarova, J., Hodinott-Hill, I., Gough, P., & Passingham, R. (2004). The Inferior Frontal Gyrus and Phonological Processing: An Investigation using rTMS. *Journal of Cognitive Neuroscience*, *16*(2), 289–300. https://doi.org/10.1162/089892904322984571

Nunez, R., Corti, D., & Retschitzki, J. (1998). Mental Rotation in Children from Ivory Coast and Switzerland. *Journal of Cross-Cultural Psychology*, *29*(4), 577–589. https://doi.org/10.1177/0022022198294005

O'Connor, D. B., Archer, J., Hair, W. M., & Wu, F. C. W. (2001). Activational effects of testosterone on cognitive function in men. *Neuropsychologia*, *39*(13), 1385–1394. https://doi.org/10.1016/S0028-3932(01)00067-7

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Ouellette, D. J., Staalduinen, E. V., Hussaini, S. H., Govindarajan, S. T., Stefancin, P., Hsu, D.-L., & Duong, T. Q. (2020). Functional, anatomical and diffusion tensor MRI study of radiology expertise. *PLOS ONE*, *15*(4), e0231900. https://doi.org/10.1371/journal.pone.0231900

Paivio, A. (1991). Dual coding theory: Retrospect and current status. *Canadian Journal of Psychology/Revue Canadienne de Psychologie*, *45*(3), 255–287. https://doi.org/10.1037/h0084295

Pamplona, G. S. P., Hardmeier, M., Younes, S., Goy, I., Fornari, E., & Ionta, S. (2022). Vision- and touch-dependent brain correlates of body-related mental processing. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *157*, 30–52. https://doi.org/10.1016/j.cortex.2022.09.005

Pang, S., Levine, L. S., Cederqvist, L. L., Fuentes, M., Riccardi, V. M., Holcombe, J. H., Nitowsky, H. M., Sachs, G., Anderson, C. E., Duchon, M. A., Owens, R., Merkatz, I., & New, M. I. (1980). Amniotic fluid concentrations of delta 5 and delta 4 steroids in fetuses with congenital adrenal hyperplasia due to 21 hydroxylase deficiency and in anencephalic fetuses. *The Journal of Clinical Endocrinology and Metabolism*, *51*(2), 223–229. https://doi.org/10.1210/jcem-51-2-223

Papeo, L., Rumiati, R. I., Cecchetto, C., & Tomasino, B. (2012). On-line Changing of Thinking about Words: The Effect of Cognitive Context on Neural Responses to Verb Reading. *Journal of Cognitive Neuroscience*, *24*(12), 2348–2362. https://doi.org/10.1162/jocn_a_00291

Pardo-Vazquez, J. L., & Fernandez-Rey, J. (2012). Working Memory Capacity and Mental Rotation: Evidence for a Domain-General View. *The Spanish Journal of Psychology*, *15*(3), 881–890. https://doi.org/10.5209/rev_SJOP.2012.v15.n3.39381

Parsons, L. M. (1987a). Imagined spatial transformation of one's body. *Journal of Experimental Psychology. General*, *116*(2), 172–191. https://doi.org/10.1037//0096-3445.116.2.172

Parsons, L. M. (1987b). Imagined spatial transformations of one's hands and feet. *Cognitive Psychology*, *19*(2), 178–241. https://doi.org/10.1016/0010-0285(87)90011-9

Parsons, L. M. (1994). Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology. Human Perception and Performance*, *20*(4), 709–730. https://doi.org/10.1037//0096-1523.20.4.709

Parsons, T. D., Larson, P., Kratz, K., Thiebaux, M., Bluestein, B., Buckwalter, J. G., & Rizzo, A. A. (2004). Sex differences in mental rotation and spatial rotation in a virtual environment. *Neuropsychologia*, *42*(4), 555–562. https://doi.org/10.1016/j.neuropsychologia.2003.08.014

Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E., & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior Research Methods*, *51*(1), 195–203. https://doi.org/10.3758/s13428-018-01193-y

Perruchoud, D., Michels, L., Piccirelli, M., Gassert, R., & Ionta, S. (2016). Differential neural encoding of sensorimotor and visual body representations. *Scientific Reports*, *6*(1), 37259. https://doi.org/10.1038/srep37259

Peters, M., Lehmann, W., Takahira, S., Takeuchi, Y., & Jordan, K. (2006). Mental Rotation Test Performance in Four Cross-Cultural Samples (N = 3367): Overall Sex Differences and the Role of Academic Program in Performance. *Cortex*, *42*(7), 1005–1014. https://doi.org/10.1016/S0010-9452(08)70206-5

Petit, L. S., Pegna, A. J., Harris, I. M., & Michel, C. M. (2006). Automatic motor cortex activation for natural as compared to awkward grips of a manipulable object. *Experimental Brain Research*, *168*(1), 120–130. https://doi.org/10.1007/s00221-005-0092-0

Petrides, M., Alivisatos, B., Evans, A. C., & Meyer, E. (1993). *Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. 90*(3), 873–877.

Pierrot-Deseilligny, C., Müri, R. M., Ploner, C. J., Gaymard, B., & Rivaud-Péchoux, S. (2003). Cortical control of ocular saccades in humans: A model for motricity. In *Progress in Brain Research* (Vol. 142, pp. 3–17). Elsevier. https://doi.org/10.1016/S0079-6123(03)42003-7

Podlogar, N., & Podlesek, A. (2022). Comparison of mental rotation ability, attentional capacity and cognitive flexibility in action video gamers and non-gamers. *Cyberpsychology: Journal of Psychosocial Research on Cyberspace*, *16*(2), Article 2. https://doi.org/10.5817/CP2022-2-8

Potvin, S., Bourque, J., Durand, M., Lipp, O., Lalonde, P., Stip, E., Grignon, S., & Mendrek, A. (2013). The Neural Correlates of Mental Rotation Abilities in Cannabis-Abusing Patients with Schizophrenia: An fMRI Study. *Schizophrenia Research and Treatment*, *2013*, 543842. https://doi.org/10.1155/2013/543842

Poulin, M., O'Connell, R. L., & Freeman, L. M. (2004). Picture recall skills correlate with 2D:4D ratio in women but not men. *Evolution and Human Behavior*, *25*(3), 174–181. https://doi.org/10.1016/j.evolhumbehav.2004.03.004

Power, J., D., Mitra, A., Laumann, T., O., Snyder, A., Schlaggar, B., L., & Petersen, S., E. (2014). *How to correct susceptibility distortions in spin-echo echo-planar images: Application to diffusion tensor imaging*. *84*, 320–341.

Power, J. D., Mitra, A., Laumann, T. O., Snyder, A. Z., Schlaggar, B. L., & Petersen, S. E. (2014). Methods to detect, characterize, and remove motion artifact in resting state fMRI. *NeuroImage*, *84*, 320–341. https://doi.org/10.1016/j.neuroimage.2013.08.048

Puts, D. A., Cárdenas, R. A., Bailey, D. H., Burriss, R. P., Jordan, C. L., & Breedlove, S. M. (2010). Salivary testosterone does not predict mental rotation performance in men or women. *Hormones and Behavior*, *58*(2), 282–289. https://doi.org/10.1016/j.yhbeh.2010.03.005

Puts, David. A., Gaulin, S. J. C., & Breedlove, S. M. (2007). *Sex differences in spatial cognition: Evolution, hormones, and the brain* (pp. 329–379). https://www.researchgate.net/publication/280579155_Sex_differences_in_spatial_cognition_Evolution_hormones_and_the_brain

Putz, D. A., Gaulin, S. J. C., Sporter, R. J., & McBurney, D. H. (2004). Sex hormones and finger length. What does 2D:4D indicate? *Evolution and Human Behavior*, *25*(3), 182–199. https://doi.org/10.1016/j.evolhumbehav.2004.03.005

Rahe, M., Ruthsatz, V., Jansen, P., & Quaiser-Pohl, C. (2018). Influence of sex-stereotyped stimuli on the mental-rotation performance of elderly persons. *Experimental Aging Research*, *44*(4), 284–296. https://doi.org/10.1080/0361073X.2018.1475156

Resnick, S. M. (1993). Sex differences in mental rotations: An effect of time limits? *Brain and Cognition*, *21*(1), 71–79. https://doi.org/10.1006/brcg.1993.1005

Resnick, S. M., Berenbaum, S. A., Gottesman, I. I., & Bouchard, T. J. (1986). Early hormonal influences on cognitive functioning in congenital adrenal hyperplasia. *Developmental Psychology*, *22*(2), 191–198. https://doi.org/10.1037/0012-1649.22.2.191

Richardson, J. T. E. (1994). Gender Differences in Mental Rotation. *Perceptual and Motor Skills*, *78*(2), 435–448. https://doi.org/10.2466/pms.1994.78.2.435

Richter, W., Somorjai, R., Summers, R., Jarmasz, M., Menon, R. S., Gati, J. S., Georgopoulos, A. P., Tegeler, C., Ugurbil, K., & Kim, S.-G. (2000). Motor Area Activity During Mental Rotation Studied by Time-Resolved Single-Trial fMRI. *Journal of Cognitive Neuroscience, 12*(2), 310–320. https://doi.org/10.1162/089892900562129

Riecanský, I., & Jagla, F. (2008). Linking performance with brain potentials: Mental rotation-related negativity revisited. *Neuropsychologia*, *46*(13), 3069–3073. https://doi.org/10.1016/j.neuropsychologia.2008.06.016

Rilling, J. K., Worthman, C. M., Campbell, B. C., Stallings, J. F., & Mbizva, M. (1996). Ratios of plasma and salivary testosterone throughout puberty: Production versus bioavailability. *Steroids*, *61*(6), 374–378. https://doi.org/10.1016/0039-128x(96)00043-8

Roberts, J. E., & Bell, M. A. (2000). Sex Differences on a Computerized Mental Rotation Task Disappear with Computer Familiarization. *Perceptual and Motor Skills*, *91*(3_suppl), 1027–1034. https://doi.org/10.2466/pms.2000.91.3f.1027

Roof, R. L., & Havens, M. D. (1992). Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Research*, *572*(1–2), 310–313. https://doi.org/10.1016/0006-8993(92)90491-q

Rotach, Z., Beazley, C., & Ionta, S. (2024). Degraded Visibility Body-Specifically Affects Mental Rotation. *Behavioral Sciences*, *14*(9), Article 9. https://doi.org/10.3390/bs14090784

Ruthsatz, V., Neuburger, S., Jansen, P., & Quaiser-Pohl, C. (2014). Pellet Figures, the Feminine Answer to Cube Figures? Influence of Stimulus Features and Rotational Axis on the Mental-Rotation Performance of Fourth-Grade Boys and Girls. In *Spatial Cognition IX* (Vol. 8684). https://www.semanticscholar.org/paper/Pellet-Figures%2C-the-Feminine-Answer-to-Cube-Figures-Ruthsatz-Neuburger/ff69a4f77bf28b9fad308dca8b2d004377c0e970

Rypma, B., Prabhakaran, V., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. E. (1999). Load-Dependent Roles of Frontal Brain Regions in the Maintenance of Working Memory. *NeuroImage*, *9*(2), 216–226. https://doi.org/10.1006/nimg.1998.0404

Sadr, M., Khorashad, B. S., Talaei, A., Fazeli, N., & Hönekopp, J. (2020). 2D:4D Suggests a Role of Prenatal Testosterone in Gender Dysphoria. *Archives of Sexual Behavior*, *49*(2), 421–432. https://doi.org/10.1007/s10508-020-01630-0

Sanchis-Segura, C., Aguirre, N., Cruz-Gómez, Á. J., Solozano, N., & Forn, C. (2018). Do Gender-Related Stereotypes Affect Spatial Performance? Exploring When, How and to Whom Using a Chronometric Two-Choice Mental Rotation Task. *Frontiers in Psychology*, *9*, 1261. https://doi.org/10.3389/fpsyg.2018.01261

Schaie, K. W. (1996). Intellectual development in adulthood: The Seattle Longitudinal Study. In *Handbook of the psychology of aging* (Vol. 4, pp. 266–286). https://www.researchgate.net/publication/246492593_Intellectual_development_in_adulthood_The_Seattle_Longitudinal_Study

Schendan, H. E., & Stern, C. E. (2007). Mental rotation and object categorization share a common network of prefrontal and dorsal and ventral regions of posterior cortex. *NeuroImage*, *35*(3), 1264–1277. https://doi.org/10.1016/j.neuroimage.2007.01.012

Scheuringer, A., & Pletzer, B. (2017). Sex Differences and Menstrual Cycle Dependent Changes in Cognitive Strategies during Spatial Navigation and Verbal Fluency. *Frontiers in Psychology*, *8*. https://doi.org/10.3389/fpsyg.2017.00381

Schöning, S., Engelien, A., Kugel, H., Schäfer, S., Schiffbauer, H., Zwitserlood, P., Pletziger, E., Beizai, P., Kersting, A., Ohrmann, P., Greb, R. R., Lehmann, W., Heindel, W., Arolt, V., & Konrad, C. (2007). Functional anatomy of visuo-spatial working memory during mental rotation is influenced by sex, menstrual cycle, and sex steroid hormones. *Neuropsychologia*, *45*(14), 3203–3214. https://doi.org/10.1016/j.neuropsychologia.2007.06.011

Schweinsburg, B., Scott, J., Dager, A., Jacobus, J., Theilmann, R., Frank, L., Weber, E., Grant, I., & Woods, S. (2012). Altered prefronto-striato-parietal network response to mental rotation in HIV. *Journal of Neurovirology*, *18*, 74–79. https://doi.org/10.1007/s13365-011-0072-z

Seghier, M. L. (2013). The Angular Gyrus. *The Neuroscientist*, *19*(1), 43–61. https://doi.org/10.1177/1073858412440596

Semrud-Clikeman, M., Fine, J. G., Bledsoe, J., & Zhu, D. C. (2012). Gender Differences in Brain Activation on a Mental Rotation Task. *International Journal of Neuroscience*, *122*(10), 590–597. https://doi.org/10.3109/00207454.2012.693999

Seurinck, R., Vingerhoets, G., de Lange, F. P., & Achten, E. (2004). Does egocentric mental rotation elicit sex differences? *NeuroImage*, *23*(4), 1440–1449. https://doi.org/10.1016/j.neuroimage.2004.08.010

Shea, D. L., Lubinski, D., & Benbow, C. P. (2001). Importance of assessing spatial ability in intellectually talented young adolescents: A 20-year longitudinal study. *Journal of Educational Psychology*, *93*(3), 604–614. https://doi.org/10.1037/0022-0663.93.3.604

Shepard, R., & Metzler, J. (1971). Mental Rotation of Three-Dimensional Objects. *Science*, *171*(3972), 701–703. https://doi.org/10.1126/science.171.3972.701

Shepard, R. N., & Cooper, L. A. (with mit press). (1986). *Mental images and their transformations*. Cambridge, Mass.: MIT Press. http://archive.org/details/MentalImag_00_Shep

Silverman, I., Choi, J., & Peters, M. (2007). The Hunter-Gatherer Theory of Sex Differences in Spatial Abilities: Data from 40 Countries. *Archives of Sexual Behavior*, *36*(2), 261–268. https://doi.org/10.1007/s10508-006-9168-6

Singh-Curry, V., & Husain, M. (2009). The functional role of the inferior parietal lobe in the dorsal and ventral stream dichotomy. *Neuropsychologia*, *47*(6), 1434–1448. https://doi.org/10.1016/j.neuropsychologia.2008.11.033

Slabbekoorn, D., van Goozen, S. H. M., Megens, J., Gooren, L. J. G., & Cohen-Kettenis, P. T. (1999). Activating effects of cross-sex hormones on cognitive functioning: A study of short-term and long-term hormone effects in transsexuals. *Psychoneuroendocrinology*, *24*(4), 423–447. https://doi.org/10.1016/S0306-4530(98)00091-2

Sorokowski, P., & Kowal, M. (2024). Relationship between the 2D:4D and prenatal testosterone, adult level testosterone, and testosterone change: Meta-analysis of 54 studies. *American Journal of Biological Anthropology*, *183*(1), 20–38. https://doi.org/10.1002/ajpa.24852

Spence, I., & Feng, J. (2010). Video Games and Spatial Cognition. *Review of General Psychology*, *14*(2), 92–104. https://doi.org/10.1037/a0019491

Stewart, J., Skvarenina, A., & Pottier, J. (1975). Effects of neonatal androgens on open-field behavior and maze learning in the prepubescent and adult rat. *Physiology & Behavior*, *14*(3), 291–295. https://doi.org/10.1016/0031-9384(75)90036-0

Surtees, A., Apperly, I., & Samson, D. (2013). Similarities and differences in visual and spatial perspective-taking processes. *Cognition*, *129*(2), 426–438. https://doi.org/10.1016/j.cognition.2013.06.008

Tagaris, G. A., Kim, S.-G., Strupp, J. P., Andersen, P., Uürbil, K., & Georgopoulos, A. P. (1996). Quantitative relations between parietal activation and performance in mental rotation. *NeuroReport*, *7*(3). https://journals.lww.com/neuroreport/fulltext/1996/02290/quantitative_relations_between_parietal_activation.22.aspx

Tan, Ü., Okuyan, M., Bayraktar, T., & Akgun, A. (2003). Covariation of Sex Differences in Mental Rotation with Body Size. *Perceptual and Motor Skills*, *96*(1), 137–144.

Tang, Z., Liu, X., Huo, H., Tang, M., Qiao, X., Chen, D., Dong, Y., Fan, L., Wang, J., Du, X., Guo, J., & Fan, Y. (2023). Sex differences in eye movements and neural oscillations during mental rotation in virtual reality. *Medicine in Novel Technology and Devices*, *18*, 100233. https://doi.org/10.1016/j.medntd.2023.100233

Tapp, A. L., Maybery, M. T., & Whitehouse, A. J. O. (2011). Evaluating the twin testosterone transfer hypothesis: A review of the empirical evidence. *Hormones and Behavior*, *60*(5), 713–722. https://doi.org/10.1016/j.yhbeh.2011.08.011

Terlecki, M. S., Newcombe, N. S., & Little, M. (2008). Durable and generalized effects of spatial experience on mental rotation: Gender differences in growth patterns. *Applied Cognitive Psychology*, *22*(7), 996–1013. https://doi.org/10.1002/acp.1420

Thakral, P. P., Madore, K. P., & Schacter, D. L. (2017). A Role for the Left Angular Gyrus in Episodic Simulation and Memory. *Journal of Neuroscience*, *37*(34), 8142–8149.

Thérien, V. D., Degré-Pelletier, J., Barbeau, E. B., Samson, F., & Soulières, I. (2022). Differential neural correlates underlying mental rotation processes in two distinct cognitive profiles in autism. *NeuroImage: Clinical*, *36*, 103221. https://doi.org/10.1016/j.nicl.2022.103221

Thomsen, T., Hugdahl, K., Ersland, L., Barndon, R., Lundervold, A., Smievoll, A. I., & Roscher, B. E. (2000). Functional magnetic resonance imaging (fMRI) study of sex differences in a mental rotation task. *Functional Magnetic Resonance Imaging*, 12.

Thomsen, T., Hugdahl, K., Ersland, L., Barndon, R., Lundervold, A., Smievoll, A. I., Roscher, B. E., & Sundberg, H. (2000). Functional magnetic resonance imaging (fMRI) study of sex differences in a mental rotation task. *Medical Science Monitor: International Medical Journal of Experimental and Clinical Research*, *6*(6), 1186–1196.

Tibon, R., Fuhrmann, D., Levy, D. A., Simons, J. S., & Henson, R. N. (2019). Multimodal Integration and Vividness in the Angular Gyrus During Episodic Encoding and Retrieval. *Journal of Neuroscience*, *39*(22), 4365–4374. https://doi.org/10.1523/JNEUROSCI.2102-18.2018

Tomasi, D., & Volkow, N. D. (2012). Laterality Patterns of Brain Functional Connectivity: Gender Effects. *Cerebral Cortex*, *22*(6), 1455–1462. https://doi.org/10.1093/cercor/bhr230

Tomasino, B., & Gremese, M. (2016). Effects of Stimulus Type and Strategy on Mental Rotation Network: An Activation Likelihood Estimation Meta-Analysis. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00693

Tomasino, B., & Rumiati, R. I. (2004). Effects of Strategies on Mental Rotation and Hemispheric Lateralization: Neuropsychological Evidence. *Journal of Cognitive Neuroscience*, *16*(5), 878–888. https://doi.org/10.1162/089892904970753

Tomasino, B., & Rumiati, R. I. (2013). Introducing the special topic "The when and why of sensorimotor processes in conceptual knowledge and abstract concepts". *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00498

Tomasino, B., Toraldo, A., & Rumiati, R. I. (2003). Dissociation between the mental rotation of visual images and motor images in unilateral brain-damaged patients. *Brain and Cognition*, *51*(3), 368–371. https://doi.org/10.1016/S0278-2626(02)00570-5

Tomasino, B., Vorano, L., Skrap, M., Gigli, G., & Rumiati, R. I. (2004). Effects of Strategies on Mental Rotation Performed by Unilateral Brain Damaged Patients. *Cortex*, *40*(1), 197–199. https://doi.org/10.1016/S0010-9452(08)70949-3

Tranel, D., Damasio, H., & Damasio, A. R. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, *35*(10), 1319–1327. https://doi.org/10.1016/s0028-3932(97)00085-7

Tustison, N. J., Avants, B. B., Cook, P. A., Zheng, Y., Egan, A., Yushkevich, P. A., & Gee, J. C. (2010). N4ITK: Improved N3 bias correction. *IEEE Transactions on Medical Imaging*, *29*(6), 1310–1320. https://doi.org/10.1109/TMI.2010.2046908

van Hemmen, J., Veltman, D. J., Hoekzema, E., Cohen-Kettenis, P. T., Dessens, A. B., & Bakker, J. (2016). Neural Activation During Mental Rotation in Complete Androgen Insensitivity Syndrome: The Influence of Sex Hormones and Sex Chromosomes. *Cerebral Cortex*, *26*(3), 1036–1045. https://doi.org/10.1093/cercor/bhu280

van Kemenade, B. M., Arikan, B. E., Kircher, T., & Straube, B. (2017). The angular gyrus is a supramodal comparator area in action–outcome monitoring. *Brain Structure and Function*, *222*(8), 3691–3703. https://doi.org/10.1007/s00429-017-1428-9

Van Maanen, L., Forstmann, B. U., Keuken, M. C., Wagenmakers, E.-J., & Heathcote, A. (2016). The impact of MRI scanner environment on perceptual decision-making. *Behavior Research Methods*, *48*(1), 184–200. https://doi.org/10.3758/s13428-015-0563-6

Vandenberg, S. G., & Kuse, A. R. (1978). Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, *47*(2), 599–604. https://doi.org/10.2466/pms.1978.47.2.599

Viana, K. M. P., Zambrana, I. M., Karevold, E. B., & Pons, F. (2016). Beyond Conceptual Knowledge: The Impact of Children's Theory-of-Mind on Dyadic Spatial Tasks. *Frontiers in Psychology*, *7*. https://doi.org/10.3389/fpsyg.2016.01635

Vingerhoets, G., de Lange, F. P., Vandemaele, P., Deblaere, K., & Achten, E. (2002). Motor Imagery in Mental Rotation: An fMRI Study. *NeuroImage*, *17*(3), 1623–1633. https://doi.org/10.1006/nimg.2002.1290

Vingerhoets, G., Santens, P., Van Laere, K., Lahorte, P., Dierckx, R. A., & De Reuck, J. (2001). Regional brain activity during different paradigms of mental rotation in healthy volunteers: A positron emission tomography study. *NeuroImage*, *13*(2), 381–391. https://doi.org/10.1006/nimg.2000.0690

Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250–270. https://doi.org/10.1037/0033-2909.117.2.250

Vuoksimaa, E., Viken, R. J., Hokkanen, L., Tuulio-Henriksson, A., Rose, R. J., & Kaprio, J. (2010). Are There Sex Differences in the Genetic and Environmental Effects on Mental Rotation Ability? *Twin Research and Human Genetics*, *13*(5), 437–441. https://doi.org/10.1375/twin.13.5.437

Wager, T. D., & Smith, E. E. (2003). Neuroimaging studies of working memory: A meta-analysis. *Cognitive, Affective & Behavioral Neuroscience*, *3*(4), 255–274. https://doi.org/10.3758/cabn.3.4.255

Wang, L., Bolin, J., Lu, Z., & Carr, M. (2018). Visuospatial Working Memory Mediates the Relationship Between Executive Functioning and Spatial Ability. *Frontiers in Psychology*, *9*. https://doi.org/10.3389/fpsyg.2018.02302

Wang, L., Cohen, A. S., & Carr, M. (2014). Spatial ability at two scales of representation: A meta-analysis. *Learning and Individual Differences*, *36*, 140–144. https://doi.org/10.1016/j.lindif.2014.10.006

Weafer, J. (2020). Sex Differences in Neural Correlates of Inhibitory Control. In H. de Wit & J. D. Jentsch (Eds.), *Recent Advances in Research on Impulsivity and Impulsive Behaviors* (pp. 73–89). Springer International Publishing. https://doi.org/10.1007/7854_2020_146

Weiss, E., Siedentopf, C. M., Hofer, A., Deisenhammer, E. A., Hoptman, M. J., Kremser, C., Golaszewski, S., Felber, S., Fleischhacker, W. W., & Delazer, M. (2003). Sex differences in brain activation pattern during a visuospatial cognitive task: A functional magnetic resonance imaging study in healthy volunteers. *Neuroscience Letters*, *344*(3), 169–172. https://doi.org/10.1016/S0304-3940(03)00406-3

Wierenga, L. M., Ruigrok, A., Aksnes, E. R., Barth, C., Beck, D., Burke, S., Crestol, A., van Drunen, L., Ferrara, M., Galea, L. A. M., Goddings, A.-L., Hausmann, M., Homanen, I., Klinge, I., de Lange, A.-M., Geelhoed-Ouwerkerk, L., van der Miesen, A., Proppert, R., Rieble, C., … Bos, M. G. N. (2024). Recommendations for a Better Understanding of Sex and Gender in the Neuroscience of Mental Health. *Biological Psychiatry Global Open Science*, *4*(2), 100283. https://doi.org/10.1016/j.bpsgos.2023.100283

Wiesen, D., Bonilha, L., Rorden, C., & Karnath, H.-O. (2022). Disconnectomics to unravel the network underlying deficits of spatial exploration and attention. *Scientific Reports*, *12*(1), Article 1. https://doi.org/10.1038/s41598-022-26491-6

Wijesinghe, R., Protti, D. A., & Camp, A. J. (2015). Vestibular Interactions in the Thalamus. *Frontiers in Neural Circuits*, *9*. https://doi.org/10.3389/fncir.2015.00079

Williams, C. L., Barnett, A. M., & Meck, W. H. (1990). Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, *104*(1), 84–97. https://doi.org/10.1037//0735-7044.104.1.84

Wolbers, T. (2003). Contralateral Coding of Imagined Body Parts in the Superior Parietal Lobe. *Cerebral Cortex*, *13*(4), 392–399. https://doi.org/10.1093/cercor/13.4.392

World Medical Association. (2013). World Medical Association Declaration of Helsinki: Ethical Principles for Medical Research Involving Human Subjects. *JAMA*, *310*(20), 2191–2194. https://doi.org/10.1001/jama.2013.281053

Wraga, M., Boyle, H. K., & Flynn, C. M. (2010). Role of motor processes in extrinsically encoding mental transformations. *Brain and Cognition*, *74*(3), 193–202. https://doi.org/10.1016/j.bandc.2010.07.005

Wraga, M., Creem, S. H., & Proffitt, D. R. (1999). The influence of spatial reference frames on imagined object- and viewer rotations. *Acta Psychologica*, *102*(2), 247–264. https://doi.org/10.1016/S0001-6918(98)00057-2

Yu, Q., Tang, Y., Li, J., Lu, Q., Wang, H., Sui, D., Zhou, L., Wang, Y., & Heil, M. (2009). Sex differences of event-related potential effects during three-dimensional mental rotation. *Neuroreport*, *20*(1), 43–47. https://doi.org/10.1097/WNR.0b013e32831c50f4

Yuan, L., Kong, F., Luo, Y., Zeng, S., Lan, J., & You, X. (2019). Gender Differences in Large-Scale and Small-Scale Spatial Ability: A Systematic Review Based on Behavioral and Neuroimaging Research. *Frontiers in Behavioral Neuroscience*, *13*. https://doi.org/10.3389/fnbeh.2019.00128

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

Zacks, J. M., & Michelon, P. (2005). Transformations of Visuospatial Images. *Behavioral and Cognitive Neuroscience Reviews*, *4*(2), 96–118. https://doi.org/10.1177/1534582305281085

Zacks, J. M., Ollinger, J. M., Sheridan, M. A., & Tversky, B. (2002). A parametric study of mental spatial transformations of bodies. *NeuroImage*, *16*(4), 857–872. https://doi.org/10.1006/nimg.2002.1129

Zacks, J., Mires, J., Tversky, B., & Hazeltine, E. (2000). Mental spatial transformations of objects and perspective. *Spatial Cognition and Computation*, *2*(4), 315–332.

Zacks, J., Rypma, Gabrieli, J. D., Tversky, B., & Glover, G. H. (1999). Imagined transformations of bodies: An fMRI investigation. *Neuropsychologia*, *37*(9), 1029–1040. https://doi.org/10.1016/s0028-3932(99)00012-3

Zapf, A. C., Glindemann, L. A., Vogeley, K., & Falter, C. M. (2015). Sex Differences in Mental Rotation and How They Add to the Understanding of Autism. *PLoS ONE*, *10*(4). https://doi.org/10.1371/journal.pone.0124628

Zeugin, D., Notter, M. P., Knebel, J.-F., & Ionta, S. (2020). Temporo-parietal contribution to the mental representations of self/other face. *Brain and Cognition*, *143*, 105600. https://doi.org/10.1016/j.bandc.2020.105600

Zhang, H., & Ekstrom, A. (2013). Human neural systems underlying rigid and flexible forms of allocentric spatial representation. *Human Brain Mapping*, *34*(5), 1070–1087. https://doi.org/10.1002/hbm.21494

Zhang, K., Fang, H., Li, Z., Tian, R., Bao-Ming, L., & Chunjie, W. (2024). Sex differences in large-scale brain network connectivity for mental rotation performance. *NeuroImage*, *298*, 120807.

Zhang, Y., Brady, M., & Smith, S. (2001). Segmentation of brain MR images through a hidden Markov random field model and the expectation-maximization algorithm. *IEEE Transactions on Medical Imaging*, *20*(1), 45–57. IEEE Transactions on Medical Imaging. https://doi.org/10.1109/42.906424