

**TO ROTATE OR NOT TO ROTATE: STRATEGY
FLEXIBILITY IN THE MENTAL ROTATION TASK**

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ABSTRACT

Rotational transformation of a mental image, or mental rotation, is a key component of spatial thinking. Yet, despite extensive research, an open question remains: is mental rotation covert simulation of motor rotation? The present work addressed this question, advancing and experimentally evaluating *the multi-strategy view of mental rotation*. This theory posits that mental rotation is covert motor simulation (claim 1) but widespread use of the mental rotation task (MRT) has obfuscated this fact. We argue that the MRT does not solely engage mental rotation but rather integrates both motoric (i.e. mental rotation) and analytic strategies that rely on visual comparison of key object features (claim 2). Three experiments examined strategy use in the MRT. In Experiment 1 we tracked physical rotation of MRT figures. Supporting the first claim, we found behavioral similarities between mental and physical rotation, suggesting comparable underlying cognitive processes. Interestingly, individuals did not rotate to a match, as is commonly assumed, but rather to an off-axis orientation. In Experiment 2 we analyzed physical rotation that mirrored covert mental rotation processes. Supporting the second claim, we found that participants differentially biased cognitive strategies based on task difficulty, preferentially using mental rotation for easy trials and analytic strategies for difficult. Experiment 3 quantified transient changes in EEG power that reflect distinct cognitive processes. Supporting the first claim, we observed sensorimotor mu suppression, a neurophysiological correlate of motor simulation and imagery, suggesting mental rotation involves covert motor simulation. Analyses of raw EEG and

independent component activations revealed that mu suppression decreased as task difficulty increased. At the same time, frontal midline theta enhancement and parietal alpha suppression increased, which reflect increased use of working memory and visuospatial representation processes, respectively. This difficulty-dependent trade-off between cognitive processes supports the second claim. We suggest that the ability to flexibly and automatically choose between mental simulation and more analytic forms of thinking is a key component of spatial intelligence. Future research should continue to consider the impact of strategies and strategy flexibility in spatial task performance. Doing so can inform domain-general processes and have real world implications across a variety of domains.

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If I have seen further it is by standing on the shoulders of giants.

– Sir Isaac Newton, *Letter to Robert Hooke (Feb. 15, 1676)*

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To Rotate or Not to Rotate: Strategy Flexibility in the Mental
Rotation Task

GENERAL INTRODUCTION

Mental images are one of the building blocks of thought. They allow us to create inner worlds, simulate past and future outcomes, and solve complex problems. But despite their name, mental images are not static entities. When one imagines their childhood home, conjuring it in their “mind’s eye,” this image is not like a photograph, hanging motionless on a gallery wall. Rather, it possesses form and dimensionality. Importantly, it can be manipulated and modified at will. Such *transformation* of mental imagery is a key component of human thought and has been studied extensively in cognitive science (Kosslyn, Thompson, & Ganis, 2006). One highly influential cognitive process that falls under this category is mental rotation, or the rotational transformation of mental images. Originally described by Shepard and Metzler (1971), the discovery of mental rotation marked a watershed moment in cognitive science. It challenged long-held behaviorist dogma by providing strong empirical evidence that cognition is subserved by mental representations. This novel theoretical framework provided a basis for a flurry of follow-up experimentation into the properties of mental imagery and its neural substrate.

Today, cognitive science is again undergoing a paradigm shift. Increasing empirical evidence supports the embodied view of cognition (Barsalou, 2008; Glenberg, 2010; Hesslow, 2002; Lakoff & Johnson, 1999; Spivey, 2007; Wilson, 2002). Like mental rotation, this view opposes prior dogma, namely that rule-based manipulation of amodal symbols underlies cognition (Fodor, 1975; Newell, 1980). Instead, embodied cognition posits that cognition is grounded in neural

systems of perception, action, and emotion and that cognitive processes are influenced by the body, including morphology and sensorimotor systems.

The term *mental rotation* suggests mental computation of a physical action. But does mental rotation engage the same cognitive processes and neural networks that underlie physical action? In other words, is mental rotation covert mental simulation of motor rotation (Wexler, Kosslyn, & Berthoz, 1998)? Increasing behavioral and neuroscientific evidence supports this notion, but contradictory evidence also exists (Zacks, 2008). The lack of consensus in the literature may stem from an assumption that the classic mental rotation task (MRT) reflects the use of a singular cognitive process, mental rotation. Instead we argue that optimal performance in the MRT depends on more than one cognitive strategy, the flexible use of which is influenced by several internal and external factors.

The Multi-Strategy View of Mental Rotation

This assertion is the basis of the *multi-strategy view of mental rotation*. This theory challenges how mental rotation has traditionally been defined in the cognitive science literature and narrows the scope of the cognitive processing it entails. According to this view, mental rotation is covert simulation of motor rotation, a motoric cognitive process that depends, in part, on neural computations in motor cortical areas that subserve motor planning and anticipation (Wexler et al., 1998). Importantly, mental rotation is not the only strategy employed in the classic MRT. Rather, the MRT engages both mental rotation as well as distinct analytic strategies that involve visual comparison but do not depend on motor

simulation. For brevity, we hereafter refer to these positions as the first and second claim of the multi-strategy view, respectively. Interpreting the mental rotation literature from this point of view helps explain the equivocal findings in the literature concerning the role of motor simulation in mental rotation and may yield novel insights about the mixture of cognitive processes and strategies that contribute to performance in the MRT. The goal of the present experiments is to gain such insights using innovative behavioral and neural techniques. But before detailing the present experiments, an overview of the classic MRT as well as empirical evidence for the multi-strategy view is needed.

Foundational Research in Mental Rotation

In a seminal study, Shepard and Metzler (1971) introduced the classic MRT (see Figure 1a and Appendix A). This task involves parity judgments of rotated abstract block figures (hereinafter referred to as SM figures). SM figure pairs are either identical (same) or mirror images (different). The classic and highly replicated findings sparked waves of both research and debate. Parity judgment response time (RT) for same figures increased monotonically and linearly with increasing angular disparity (see Figure 1b). In other words, the greater the rotational difference between the identical SM figures the longer individuals took to judge them the same. We refer to this linear function as the angular disparity effect (ADE). The authors interpreted this finding as strong evidence that individuals rotated analogous mental images of the SM figures until aligned to match. The logic was that mental rotation involved first forming a mental image of one SM figure and then imagining that figure rotating through

intermediate orientations until aligned with the comparison figure. Assuming constant rotational speed, rotation-to-match would take more time for larger angular disparities, just as with physical rotation.

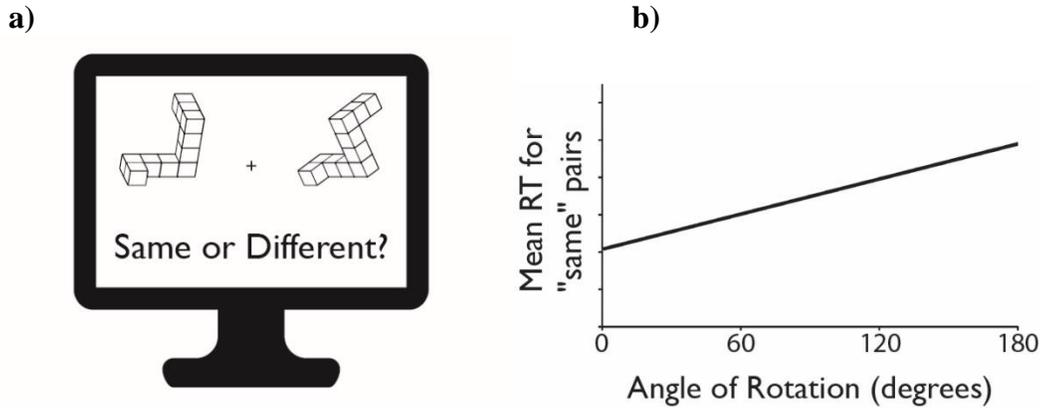


Figure 1. An example MRT trial (a) and the classic behavioral hallmark of mental rotation, the ADE, a linear increase in RT as a function of angular disparity (b).

The discovery of mental rotation suggested that analog spatial representations can underlie cognition (Shepard & Cooper, 1982), a point that engendered much controversy, such as the well-known mental imagery debate (Kosslyn et al., 2006; Pylyshyn, 2003). This debate is outside the scope of this dissertation. However, this seminal experiment yielded other implicit assumptions that are directly relevant to the present work, namely that individuals mentally rotate objects in the same manner that they would physically and that individuals universally apply this strategy. The multi-strategy view posits that mental rotation is covert simulation of motor rotation, in line with the first assumption. However, this strategy is *not* universally applied in the MRT. Rather, mental rotation, involving the physical-like rotation of an analog mental image, is flexibly employed in the MRT.

Flexible Strategy Use in the MRT

Considerable research supports flexible strategy use in the MRT.

Discussion of different strategies emerged in the wake of Shepard and Metzler's (1971) findings. Mental rotation research first drew a distinction between holistic and piecemeal processing, the application of which depends on numerous factors, including stimulus familiarity, meaningfulness, and complexity (Folk & Luce, 1987; Just & Carpenter, 1976; Just & Carpenter, 1985; Kail, Pellegrino, & Carter, 1980; Kail, 1985; Kail, 1986; Mumaw, Pellegrino, Kail, & Carter, 1984; Shepard & Metzler, 1988). Holistic processing involves rotation of the mental image as an analogous whole, akin to the process proposed by Shepard and Metzler (1971). In contrast, piecemeal processing involves decomposing the mental image into constituent parts and then serially rotating all or some of the pieces into congruence with the comparison figure. Classic studies investigated these strategies by manipulating object complexity, but yielded mixed results. Some work found no effects of increased stimulus complexity on mental rotation speed, suggesting holistic processing (Cooper & Shepard, 1975; Cooper & Podgorny, 1976) while others found slowing, suggesting piecemeal processing (Folk & Luce, 1987; Yuille & Steiger, 1982). This holistic-piecemeal distinction continues to motivate empirical work on mental rotation (Khooshabeh, Hegarty, & Shipley, 2013; Liesefeld, Fu, & Zimmer, 2014). Other work suggests viewpoint-independent strategies in the MRT. Such analytic strategies do not require mental rotation, but instead involve examining internal relations between stimuli parts independent of their orientation (Bethell-Fox & Shepard, 1988; Geiser, Lehmann,

& Eid, 2006; Glück & Fitting, 2003; Just & Carpenter, 1985). For example, one can compare SM figures by encoding the number of constituent blocks and the series of turns connecting those blocks in each figure.

The idea that the MRT can involve multiple strategies is further supported by theoretical work. This research suggests that individuals bias strategies in the MRT dynamically based on numerous factors, including individual differences, stimuli differences, and task difficulty. Schultz (1991) probed participants' cognitive strategies with spatial tasks, including the MRT. During each task, participants were repeatedly interrupted and asked to write down how they were solving the problem. Two strategies in the MRT emerged from these reports: a mental rotation strategy, involving imagined movement of the stimuli, and an analytic strategy, involving identification of key visual features of the stimuli and observation of their presence, absence, or change. A similar distinction between holistic mental rotation and analytical strategies in the MRT was proposed by Cooper (1976). Importantly, Schultz (1991) found that strategy use was heterogeneous both between and within participants. Rather than use one strategy, participants *dynamically* switched strategies from trial to trial. It should be noted that the authors also identified a third strategy, perspective change, involving self-movement that was flexibly used in other spatial tasks but not in the MRT.

Likewise, Just & Carpenter (1985) identified and investigated several cognitive strategies employed in a cube comparison task including mental rotation and analytic orientation-free descriptions. Participants tended to use mental rotation overall but some reported using an orientation-free analytic strategy that

involved coding relations between stimuli features and then comparing these relations between stimuli. Geiser et al. (2006) drew similar conclusions by applying latent class analysis in the MRT. They too identified both holistic mental rotation strategies and an analytic non-rotation strategy involving visual feature comparison. In light of these findings and others, two basic components have been proposed to underlie spatial intelligence, a mental imagery or simulation strategy and an analytic or rule-based strategy. Optimal performance on spatial tasks in turn depends on flexibly biasing these strategies (Hegarty, 2010). Taken together, this research suggests that single processing models that posit a one-size-fits-all cognitive process are inadequate in explaining performance in spatial tasks, such as the MRT. Rather, strategy-shift models that integrate multiple strategies are preferable (Botella, Peña, Contreras, Shih, & Santacreu, 2009; Glück & Fitting, 2003; Kyllonen, Lohman, & Woltz, 1984; Lohman, 1988).

Additionally it is important to note that more than one strategy may underlie mental rotation itself. Recent theory suggests that mental rotation can be subdivided into different strategies. The multiple systems framework (Zacks & Michelon, 2005), posits that transformation of visuospatial mental images involves updating specific reference frames in relation to other reference frames. These reference frames include object-centered reference frames, defined relative to external objects, egocentric reference frames, defined relative to the self, and environmental reference frames, defined relative to fixed environment features. Within the domain of mental rotation, two types of transformation are distinguished. Object-based transformation involves updating an object's

reference frame relative to the other frames, in other words, mentally simulating an object *rotating by itself*. Effector-based transformation involves updating one's effector-centered reference frame relative to the other frames, in other words mentally simulating an object *rotating due to manual interaction*. Which mental rotation sub-strategy is preferentially used is influenced by experiment factors such as the stimuli used or the instructions given (Zacks, 2008).

Concerning the multi-strategy view, both transformations can be considered covert motor stimulation as they both involve the simulation of actual rotation without overt physical movement. As such, in the present dissertation we often combine both strategies under the mental rotation heading. However, while both sub-strategies have been associated with activation in motor cortical areas, including the primary motor, premotor, and supplementary motor cortices, activation patterns in these areas differ between strategies (Tomasino & Gremese, 2015). Specifically effector-based (motor) rotation elicits greater primary motor cortical activation than object-based (visual) rotation, likely due to mental simulation of one's own hand that co-occurs with effector-based rotation. However, both strategies have been shown to elicit activation in premotor areas that are related to planning and anticipation of movement, supporting the claim that mental rotation involves covert motor simulation. Variable activation patterns between mental rotation sub-strategies combined with the context-sensitive use of these sub-strategies and non-rotation-based analytic strategies have complicated empirical investigations of mental rotation and contributed to a complex and varied literature.

One issue emergent from this literature concerns the role of motor simulation in mental rotation (Zacks, 2008). While increasing behavioral and neuroscientific evidence suggests that mental rotation depends on covert motor simulation, other findings do not support this view. We argue that adopting a strategy-shift model can help interpret these inconsistent findings. In the next section, we review empirical evidence that suggests mental rotation causally engages the motor system, supporting the first claim of the multi-strategy view. Then we review how experimental design factors influence cognitive strategy use in the MRT, lending support for the second claim.

Motor Simulation and Mental Rotation

Experiments using physical interference paradigms have demonstrated that mental rotation interacts with physical action. In these experiments, participants complete a MRT while simultaneously turning a knob or joystick (Wexler et al., 1998; Wohlschläger & Wohlschläger, 1998). The central finding shows that manual rotation in the same direction as mental rotation (to a match) decreases RT in the MRT. In contrast, when manual and mental rotation directions are incongruent, RTs increase (but see: Sack, Lindner, & Linden, 2007). Interestingly, merely planning a rotational hand movement is enough to influence MRT performance (Wohlschläger, 2001). It is important to note that directional manual actions do not always yield direction-congruent outcomes. For example, when flying a plane, pulling *down* on the yoke (joystick) causes the plane's nose to move *upwards*. In such cases manual-mental interactions arise from the congruency of the mentally-simulated outcomes (Janczyk, Pfister,

Crognale, & Kunde, 2012). These interactive effects suggest similar underlying cognitive processes. Other research using training paradigms has demonstrated that training manual object rotation improves subsequent MRT performance in both adults (Wiedenbauer, Schmid, & Jansen-Osmann, 2007) and children (Wiedenbauer & Jansen-Osmann, 2008). Even coordinative motor ability training can improve MRT performance (Blüchel, Lehmann, Kellner, & Jansen, 2013; Jansen, Titze, & Heil, 2009). Taken together, these findings support the idea that motor simulation plays a causal role in mental imagery transformation.

Complementary support comes from gesture research. Gestures influence thought by linking action with mental representations (Goldin-Meadow & Beilock, 2010). This linkage enhances spatial problem solving (Chu & Kita, 2011b). During the MRT gesture initially reflects the agentive manipulation one might enact when physically rotating the objects. Over time, knowledge gained through gesture is internalized and individuals need not rely on gesture any longer (Chu & Kita, 2008). An initial reliance on gesture and subsequent internalization has also been observed during spatial reasoning of gear movements (Hegarty, 2004; Hegarty, Mayer, Kriz, & Keehner, 2005; Schwartz & Black, 1996). Further, gesture's influence in the MRT is robust and causal. Restricting gesture production impairs MRT performance and knowledge gained from gesturing in the MRT transfers to other novel spatial tasks (Chu & Kita, 2011a). Gestures likely interact with MRT performance by aiding the use of perceptuo-motor strategies (i.e. mental rotation) (Alibali, Spencer, Knox, & Kita, 2011; Hostetter, Alibali, & Bartholomew, 2011).

Neuroscience findings likewise generally support the first claim. Because of its significance to the mental imagery debate (Kosslyn et al., 2006; Pylyshyn, 2003), mental rotation is one of the most studied higher-order cognitive processes in cognitive neuroscience. If the first claim is true then mental rotation should consistently activate the brain's motor areas. Yet, neuroimaging research has been equivocal on this point. In a meta-analysis of over 30 neuroimaging studies, Zacks (2008) drew two conclusions concerning the neural substrate of mental rotation. First, mental rotation consistently activates posterior parietal cortex. This area subserves action-oriented mental image generation and maintenance as well as represents spatial maps for targets of goal-oriented action. Second, and of direct relevance for the multi-strategy view, mental rotation frequently (but *variably*) activates motor areas, including primary motor cortex (M1), premotor cortex (PMC), and the supplementary motor area (SMA). These areas are broadly involved in the planning, anticipation, and execution of movements. M1 activation is related to simple movement execution and is thought to represent low level attributes of movement such as hand position and velocity (Paninski, Fellows, Hatsopoulos, & Donoghue, 2004; Sanes & Donoghue, 2000). PMC and SMA activation are also thought to play a role in movement execution but importantly also in internally-generated sequential movement planning and preparation as well as motor imagery (Héту, Grégoire, Saimpont, & Coll, 2013; Hoshi & Tanji, 2007; Nachev, Kennard, & Husain, 2008). These two secondary motor regions appear to subtly differ in their contributions to sequential movement control and recent work suggests that PMC may critically underlie

performance of spatial movement sequences while SMA may underlie temporal sequences (Ohbayashi, Picard, & Strick, 2016; Tanji, 2001). Variably observed activation in these motor areas in MRT-based studies likely reflects *flexible* recruitment of mental rotation (i.e. motor simulation) as well as its sub-strategies (effector- vs. object-based rotation) based on stimuli affordances and strategy differences. Behavioral research, reviewed below, similarly suggests variable motor simulation in the MRT.

At first glance this variability appears to cast doubt on the first claim. How can mental rotation causally engage the motor system given this mixed neural evidence? The answer is to appeal to the second claim which posits that the MRT dynamically engages several cognitive strategies. These strategies include mental rotation, which involves covert simulation of motor rotation, but also distinct analytic strategies that do not. In light of the multi-strategy nature of the MRT, we argue that cognitive processing in the MRT is best explained by a strategy-shift model (Kyllonen et al., 1984). Such models predict that internal and external factors should influence when mental rotation is used. This prediction is borne out in the mental rotation literature. As reviewed below, different stimuli, task framing, individual differences, and task difficulty all influence the extent to which mental rotation is used in the MRT. We suggest that these factors influence the MRT's *strategy profile*, the set of cognitive strategies that individuals bring to bear and the ways they bias these strategies. Considering the impact of the following factors on MRT strategy profiles rather than mental rotation itself helps

explain the equivocal findings concerning the causal link between motor simulation and mental rotation.

Factors Influencing Motor Simulation in the MRT

Stimuli. Stimuli used in the MRT differ in the extent to which they implicitly bias motor simulation. The classic MRT presents abstract shapes or SM figures (Shepard & Metzler, 1971; Shepard & Cooper, 1982) but other seminal research has used pictures of hands. Mental rotation of hands is thought to involve mentally simulating the rotation of one's own hands, an embodied cognitive process that inherits the kinesthetic and biomechanical constraints of the human body (Decety, 1996; Jeannerod, 1994; but see: Steenbergen, Nimwegen, & Crajé, 2007; Vannuscorps, Pillon, Andres, 2012). Indeed, behavioral experiments have shown that corporeal stimuli, such as hands and bodies, consistently, automatically, and forcefully recruit such effector-based motor simulations (Krüger, Amorim, & Ebersbach, 2014). Further, M1 activation functionally subserves mental rotation of these stimuli but this is not necessarily the case for non-corporeal stimuli, such as letters or SM figures (Ganis, Keenan, Kosslyn, & Pascual-Leone, 2000; Tomasino, Borroni, Isaja, & Ida Rumiati, 2005; Tomasino, Budai, Mondani, Skrap, & Rumiati, 2005; but see: Bode, Koeneke, & Jancke, 2007).

Task Framing. Experiment-level factors also influence strategy use in the MRT. The extent to which participants use mental rotation and its sub-strategies in the MRT can be influenced by implicit priming or by explicit task directions (Kosslyn, Thompson, Wraga, & Alpert, 2001; Wraga, Thompson, Alpert, &

Kosslyn, 2003). For example, Kosslyn et al. (2001) primed mental rotation sub-strategies by having participants either manually rotate SM figures (effector-based) or passively watch them rotate by an electric motor (object-based) prior to completing a figural MRT. The effector-primed group elicited greater M1 activation (likely SMA, see Zacks, 2008) in the MRT than the object-primed group. However, when compared to baseline, both conditions yielded PMC activation, consistent with the idea that both mental rotation sub-strategies can be considered covert motor rotation. In addition, task framing caused by experiment instructions is a strong manipulation and can overcome existing stimuli biases (Flusberg & Boroditsky, 2011) as well as modify cortical processing. For example, M1 appears to functionally subserve mental rotation only when a manual/effector-based strategy is explicitly instructed (Tomasino et al., 2005; Tomasino, Skrap, & Rumiati, 2011).

Individual Differences. Individual differences are frequently discussed in the mental rotation literature. With regards to MRT strategies, three factors appear to play a large role: sensorimotor experience/ability, gender, and age.

Motor Experience and Ability. Motor-experienced individuals, such as athletes, show enhanced mental rotation performance (Habacha, Molinaro, & Dosseville, 2014; Heinen, 2013; Jansen & Lehmann, 2013). This “athlete advantage” likely stems from a bias to use mental rotation in the MRT (Amorim, Isableu, & Jarraya, 2006; Moreau, Mansy-Dannay, Clerc, & Guerrien, 2011; Moreau, 2012; Moreau, 2013; Moreau, 2014; Tomasino, Maieron, Guatto, Fabbro, & Rumiati, 2013). Experimental evidence suggests athletes use mental

rotation even when the stimuli do not explicitly afford it, such as is the case with SM figures (but see: Kaltner, Riecke, & Jansen, 2014; Steggemann, Engbert, & Weigelt, 2011). On the other end of the spectrum, motor-impaired individuals show deficits in the MRT. Individuals with Parkinson's disease (PD) as well as patients with chronic and temporary vestibular degradation or loss show impairments in the MRT compared to neurotypical controls (Amick, Schendan, Ganis, & Cronin-Golomb, 2006; Candidi et al., 2013; Crucian et al., 2003; Lee, Harris, & Calvert, 1998; Picazio, Oliveri, Koch, Caltagirone, & Petrosini, 2013; Péruch et al., 2011; ter Horst, Cole, Van Lier, & Steenbergen, 2012; Wallwork, Butler, & Moseley, 2013).

Gender. Gender effects are frequently observed in the MRT, with males outperforming females (Linn & Petersen, 1985; Miller & Halpern, 2014; Voyer, Voyer, & Bryden, 1995). Yet, the source of these effects remains an open question in the mental rotation literature. Strategy differences may play a role (Butler et al., 2006; Bryden, 1980; diSessa, 2004; Glück & Fitting, 2003; Voyer & Saunders, 2004). For example, recent research suggests males and females bias strategies in the MRT differently. As mentioned previously, MRTs using corporeal stimuli, such as hands or bodies, consistently recruit effector-based mental rotation. In such corporeal-MRTs gender differences disappear (Alexander & Evardone, 2008, but see: Voyer & Jansen, 2015). Related neuroscientific evidence shows that while neural activation during mental rotation of SM figures differs between genders (Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002), activation patterns for hand and tool stimuli are largely similar (Seurinck,

Vingerhoets, de Lange, & Achten, 2004). Likewise, in a simple cognitive task that strongly favors mental rotation not only do males and females perform equally well but females produce less neural activation, suggesting more efficient neural information processing (Christova, Lewis, Tagaris, Uğurbil, & Georgopoulos, 2008). These findings suggest that females are similar to males regarding mental rotation but differ with respect to analytic strategies that primarily rely on visual comparisons. In other words, they have different strategy profiles, with females biasing mental rotation overall. This predilection may disadvantage females by de-emphasizing alternative analytic strategies when such strategies are optimal (Hegarty, 2010; but see: Janssen & Geiser, 2010).

Age. MRT strategy profiles also appear to differ with respect to age. Several lines of research suggest that children and infants are capable of mental rotation and do so primarily by mentally simulating physical action (Frick, Möhring, & Newcombe, 2014). MRT performance improves for 6-month old infants after manual exploration (Möhring & Frick, 2013), for 4-year olds when they are instructed to gesture (Ping, Ratliff, Hickey, & Levine, 2011), and for 8- to 10-year old children after two weeks of coordinative motor training (Blüchel et al., 2013). Children are also particularly susceptible to motor interference in the MRT. 5- and 6-year old children's MRT performance for hand stimuli is influenced by the static posture of their own hands (Funk, Brugger, & Wilkening, 2005). On the other end of the spectrum, older adults perform worse in the MRT than younger adults (Dror & Kosslyn, 1994; Hertzog, Vernon, & Rypma, 1993; Saimpont, Pozzo, & Papaxanthis, 2009). These deficits seem related to

impairment in mental rotation and are related to motor ability (De Simone, Tomasino, Marusic, Eleopra, & Rumiati, 2013; Jansen & Kaltner, 2014).

Task Difficulty

Task difficulty also influences strategy profiles in the MRT (Glück & Fitting, 2003). Difficulty in the MRT is operationalized as the angular disparity between stimuli. Since the behavioral hallmark of mental rotation is a positive linear relationship between RT and angular disparity (i.e. an ADE), all mental rotation experiments dynamically manipulate task difficulty trial by trial. Therefore task difficulty is perhaps the most significant factor that impacts MRT strategies because it is a ubiquitous manipulation in the literature. Early psychometric research using spatial tasks suggests that both strategy variability and bias for analytic or non-spatial strategies increase with task difficulty (Barratt, 1953; Myers, 1957). Mental rotation is biased for easy trials while analytic strategies are biased for difficult trials (Cochran & Wheatley, 1989; Lohman & Kyllonen, 1983). Gesture research supports this assertion. Individuals are more likely to spontaneously produce gestures for difficult MRT trials, suggesting that under such conditions an internalized mental rotation strategy is difficult to adopt (Chu & Kita, 2011a).

Neuroscientific evidence also lends support, demonstrating that cortical activations in the MRT vary due to task difficulty. Increasing task difficulty is associated with increasing activation in posterior parietal and higher-order premotor areas and decreasing activation in the SMA (Carpenter, Just, Keller, Eddy, & Thulborn, 1999; Milivojevic, Hamm, & Corballis, 2009). Increasing

PMC activation may play a supplementary role related to visualization of hidden parts of the mental image, represented in the PPC (Kawamichi, Kikuchi, Noriuchi, Senoo, & Ueno, 2007; Kawamichi, Kikuchi, & Ueno, 2007), while decreasing SMA activation may reflect decreasing use of covert motor simulation. Similarly, connectivity of brain areas varies due to MRT task demands. Under increased task difficulty, functional coupling of a visual pathway increases while coupling of a motoric pathway decreases (Ecker, Brammer, & Williams, 2008), suggesting decreased mental rotation and increase analytic strategy use with increasing difficulty.

The idea that task difficulty influences strategy profiles should receive special consideration given that the behavioral hallmark of mental rotation is the ADE. As a result not only do all mental rotation experiments manipulate task difficulty to yield ADEs but importantly many do not consider it a variable that may influence strategy use. However, the behavioral and neuroscientific evidence reviewed above suggests that easy trials in the MRT bias mental rotation while difficult trials bias analytic strategies. Thus task difficulty may be a significant but under-explored factor in mental rotation research.

Dissociating the Mental Rotation Process from the Task

The research reviewed above suggests that the MRT does not solely engage mental rotation. Rather, individuals bias strategies depending on individual differences and task stimuli, framing, and difficulty. These strategies include holistic mental rotation but also analytic strategies, such as visual comparison of key stimuli features, counting, or verbal coding. Applying a

strategy-shift model to the MRT provides a theoretical basis for the equivocal findings concerning motor simulation in the literature because such models predict variability due to experimental design differences. However, a strategy-shift model lends only indirect support for the claim that mental rotation causally engages the motor system.

Recent work has used novel methodologies and carefully controlled for confounding factors in the MRT to isolate the mental rotation cognitive process. For example, a limitation of neuroimaging studies of mental rotation is that they commonly require manual button presses for responding. Observation of M1 activation may be epiphenomenal of this response (Richter et al., 2000; Windischberger, Lamm, Bauer, & Moser, 2003; Zacks, 2008). However, when manual responses are not required, M1 excitability, as measured by motor evoked potentials, is still observed during mental rotation (Bode et al., 2007; Eisenegger, Herwig, & Jäncke, 2007). This activation likely reflects spill-over activation from adjacent PMC. Further, as discussed previously, the MRT combines non-rotational cognitive processes, including stimulus encoding, mental image generation, and stimulus comparison, with mental rotation proper. However, when mental rotation is examined in isolation, using time-resolved fMRI, PMC activation is consistently observed (Ecker et al., 2008; Lamm, Windischberger, Moser, & Bauer, 2007; Richter et al., 2000). Similar findings have been recently found using simultaneous electroencephalography (EEG) and fMRI (Sasaoka, Mizuhara, & Inui, 2014). Previous research demonstrated suppression of beta-band power at left frontal and bilateral parietal sites during mental rotation

(Williams, Rippon, Stone, & Annett, 1995). Sasaoka and colleagues had participants complete a modified mental clock task, mentally rotating clock hands at constant speed. Consistent with previous research, the researchers found beta EEG suppression was associated with increases in amount of rotation, providing an electrophysiological marker of mental rotation. The authors then identified brain regions that were correlated with temporal fluctuations in beta suppression, using fMRI. Combining EEG and fMRI analyses in this way revealed a dynamic cortical network associated with mental rotation that included the left PMC and bilateral parietal cortices. These results suggest that mental rotation is subserved by neural computations in the PMC which in turn transform and update the imagined clock hands represented in the parietal cortex. Taken together, recent research that takes steps to isolate mental rotation provides strong evidence that mental rotation relies on covert motor simulation that depends on neural computations in motor cortical areas that subserve motor planning and anticipation. These studies, which consider and control for confounding factors in the MRT, consistently yield motor cortical activation during mental rotation and support the multi-strategy view.

Conclusions and Motivation for Dissertation

The multi-strategy view and the supporting research reviewed above lead to the following conclusions. First, the MRT does not solely engage mental rotation but rather several dynamically-used strategies. We refer to this set of strategies and how individuals bias them as a *strategy profile*. Second, one of the strategies deployed in the MRT is mental rotation and empirical evidence

suggests that this cognitive process is covert motor rotation and depends on neural computations in motor cortical areas. Third, several internal and external factors influence when individuals use mental rotation in the MRT. One of the most significant of these is task difficulty. It is manipulated in all MRT-based experiments and some empirical evidence suggests it influences strategy profiles in the MRT.

Following from these conclusions, the present dissertation seeks to better understand mental rotation and the different cognitive strategies used in the MRT. If mental rotation is covert motor rotation then observing physical rotation may yield novel insights into mental rotation. To date little research has directly compared physical and mental rotation in the MRT. Experiment 1 addresses this need by utilizing a novel physical rotation behavioral task. Experiment 2 complements and extends Experiment 1 by critically examining the role of task difficulty and how it impacts MRT strategy profiles inferred from physical rotation. Lastly, Experiment 3 expands this investigation by using EEG to observe motor cortex activation as well as other neurophysiological markers of cognitive processing in the MRT. Together, these experiments investigate and clarify the role of motor simulation in mental rotation and yield insight into the mixture of cognitive strategies that contribute to MRT performance, supporting the multi-strategy view.

EXPERIMENT 1

Introduction

In light of the assumption that mental rotation is covert motor rotation, it is important to directly compare mental and physical rotation. This comparison allows the exploration of central assumptions in the mental rotation literature, namely that mental rotation involves rotating mental images analogous to physical objects to match their orientations and that similar cognitive processes underlie mental and physical rotation. Limited research has directly compared mental and physical rotation. Studies using physical interference paradigms have shown that incongruent physical rotation, hand immobilization, and forbidding manual gesture production impair mental rotation (Chu & Kita, 2011a; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Moreau, 2013; Wexler et al., 1998). Other behavioral work suggests similarities between mental and physical rotation. Wohlschläger and Wohlschläger (1998) compared RTs for a classic MRT and a physical rotation task (PRT) in which participants rotated three-dimensional (3-D) figures by turning a dial. The tasks yielded statistically indistinguishable ADEs. Two inferences emerge from these findings. First, overlapping cognitive processes underlie mental and physical rotation. Second, given this overlap, insight into mental rotation may be gained from observation of physical rotation.

In Experiment 1 we directly compared behavioral performance in a classic MRT and a novel PRT using virtual 3-D SM figures, a novel tri-axis rotational apparatus, and real-time physical rotation data collection. We predicted that the tasks would yield behavioral similarities. Specifically, RTs for both tasks would

yield ADEs, replicating Wohlschläger and Wohlschläger (1998). Further, we predicted participants' real-time physical rotation in the PRT would reflect rotation to a matching mental image, in line with the classic assumption introduced by Shepard and Metzler (1971) that is largely agreed upon in the mental rotation literature.

Method

Participants & Design

Thirty-two Tufts University undergraduates (mean age = 19.5 years; 16 male, 16 female) participated for monetary compensation.

Materials

Figures and Stimuli Presentation. We designed 3-D models of SM figures from Peters and Battista's (2008) stimulus library using Google SketchUp (<http://google-sketchup.en.softonic.com/>). The stimuli (15 figures and their mirror images) were presented using virtual-reality software (WorldViz Vizard 4.0, Santa Barbara, CA). Figure 2a depicts our experimental setup, showing how stimuli were presented. In the PRT, participants rotated figures using a handheld rotational sensor with three degrees of freedom, the Intersense InertiaCube 2+ (Boston, MA), encased in a tennis ball. This spherical rotation apparatus (see Figure 2b) minimized imposition of reference frames, although the data cable may have imposed some awkwardness. However, neither participant report nor experimenter observation suggested any impact of awkwardness.

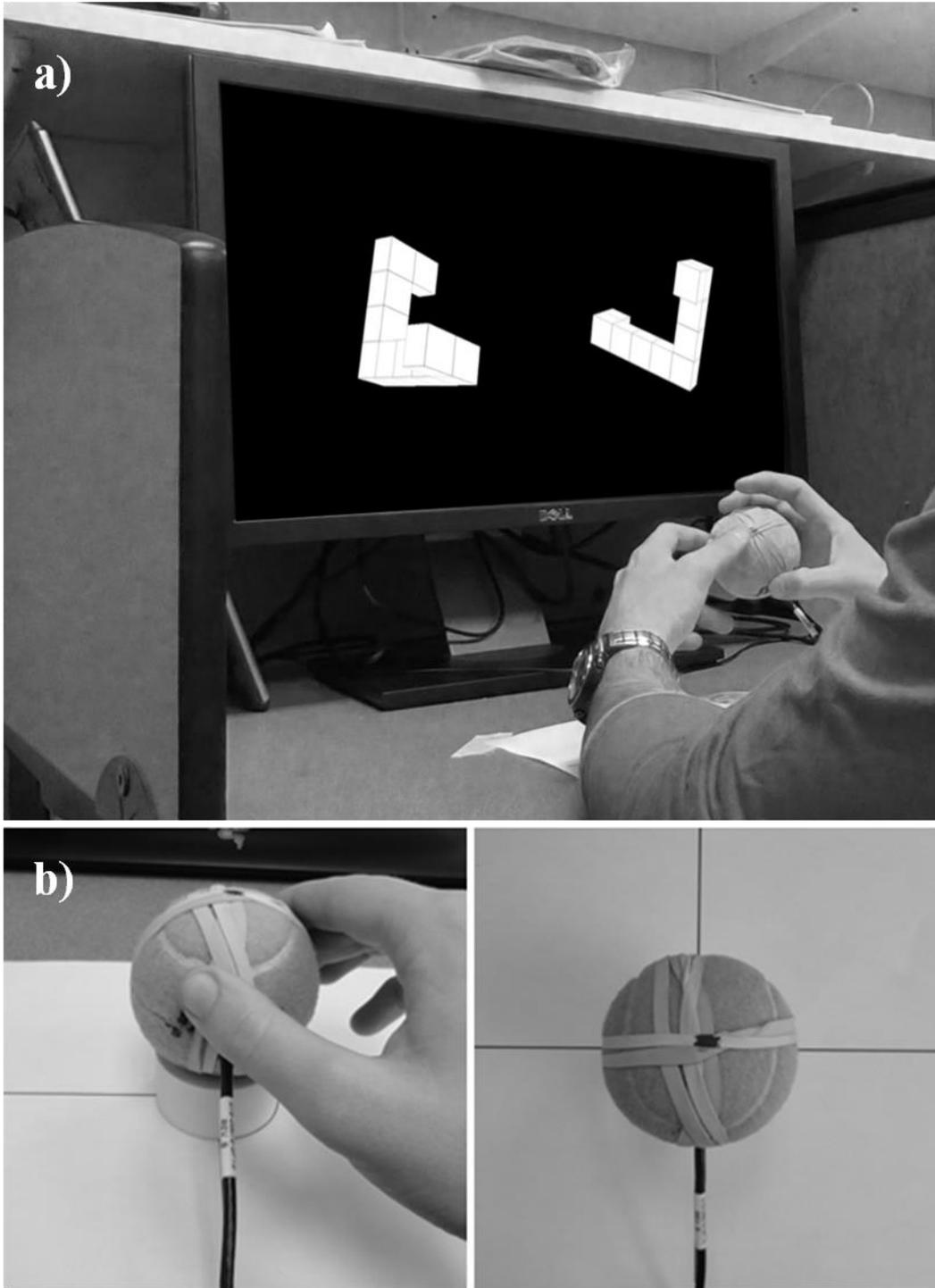


Figure 2. Experimental setup (a) and close-ups of the rotation apparatus (b) used in Experiment 1. Used with author permission from Gardony, Taylor, & Brunyé, 2014.

Questionnaires and Cognitive Assessments. We assessed factors related to mental rotation performance: spatial ability; preferences for landmark-based (i.e., a focus on unique objects at constant locations), route-based (i.e., a focus on sequences of paths and turns), and survey-based (i.e., a focus on abstracting knowledge from sequences into a global model) spatial representation; spatial self-confidence; preferences for survey strategies; knowledge of cardinal directions; video game experience; and working memory capacity. Table 1 lists the measures used to assess each variable, as well as the results for our sample.

Table 1. Experiment 1, individual difference measures.

Individual Difference	Questionnaire/Assessment	Statistics & Interpretation
Spatial ability	Santa Barbara Sense of Direction Scale (Hegarty, Richardson, Montello, Lovelace, & Subbiah, 2002)	Moderate sense of direction $M = 4.1$, scale: 1 - 7
Preferences for landmark, route, and survey-based spatial mental representation	Spatial Representation Questionnaire (Pazzaglia & De Beni, 2001)	Landmark and route representation preference over survey $M_L = 7.3$, $M_R = 7.1$, $M_S = 5.8$, scale: 2 - 10
Spatial self-confidence, survey strategy, and knowledge of cardinal directions	English FRS questionnaire on spatial strategies (Münzer & Hölscher, 2011)	Moderate self-confidence in spatial abilities $M = 4.3$, scale: 1 - 7 Moderate preference for survey strategies $M = 3.7$, scale: 1 - 7 Low knowledge of cardinal directions $M = 2.4$, scale: 1 - 7
Video game experience	Video game experience questionnaire (Boot, Kramer, Simons, Fabiani, Gratton, 2008)	Moderate video game frequency $M = 1.8$ hours per week
Working memory capacity (WMC)	OSPAN (Turner & Engle, 1989; Kaufman, 2007)	Moderate WMC $M = 38$ (hypothetical range = 0 - 64)

Procedure

Participants first completed the questionnaires and an operation span task. In both experimental tasks, participants saw two SM figures presented side by side on a monitor. One figure was designated the target and the other the response figure. The figures in each pair were presented in different rotations, and participants had to judge whether the two figures were identical (same) or mirror images of each other (different). In the MRT participants mentally rotated the response figure and in the PRT they actually rotating it using the bimanually held sensor. Participants were instructed to respond quickly and accurately, saying “same” or “different” into a headset microphone. Microsoft Speech SDK voice-recognition software recorded their responses.

The presentation order of the MRT and PRT and the response figure’s screen position (left, right) were equally counterbalanced across male and female participants. Five practice trials that used figures distinct from those in the main experiment preceded each task. For the MRT, participants practiced mentally rotating the response figure; for the PRT, they practiced rotating the response figure with the sensor. The main task involved three trial blocks, each containing 15 same and 15 different trials in which the figures were randomly selected (without replacement) from the stimulus set. Each trial presented figure pairs in random rotations. The angular difference (in degrees) between the figures’ quaternion rotations (see Hanson, 2006, for a review) was sampled from a uniform distribution between 0 and 180. A quaternion represents 3-D rotation as a vector between a sphere’s center and a point on its surface, and the angular

difference (henceforth referred to as the angular disparity) represents the angle required to rotate one figure into congruence with another. Using quaternions, instead of Euler angles, avoids aberrant tri-axis rotational behavior (e.g., gimbal lock) and provides an easy-to-interpret measure of angular disparity (see Appendix B for equations used to calculate angular disparity). Trials were separated by a screen instructing participants to continue to the next trial; for PRT trials, the screen additionally instructed participants to return the sensor to the starting position. Saying “next” began a new trial. Error rates, RTs (time-locked to voice onset), and real-time angular disparities (for the PRT; 50 Hz) were recorded. Upon completion of the main task, participants were debriefed and compensated.

Results

We considered only correct responses in our analyses of RT and continuous PRT data. We first examined the MRT and PRT for the classic ADE. For each participant, we correlated the initial angular disparities between figure pairs and RTs for same trials. Both the MRT and PRT yielded ADEs. Pearson correlation coefficients (MRT: mean $r = .36$, PRT: mean $r = .32$) differed significantly from zero — MRT: $t(31) = 12.62, p < .001$, PRT: $t(31) = 10.79, p < .001$, and a paired t test comparing the correlation sets was not significant, $t(31) = 1.04, p > .1$, which suggests that ADEs were similar in both tasks.

We further examined how RTs and error rates varied at different initial angular disparities. We employed repeated measures analyses of variance (ANOVAs), with Greenhouse-Geisser correction in the case of sphericity

violations (Geisser & Greenhouse, 1958), denoted by F_{GG} . We divided trials with different initial angular disparities into six 30° bins and submitted RTs to a 2 (task: MRT, PRT) × 2 (trial type: same, different) × 6 (initial angular disparity bin: 0°–30°, 30°–60°, 60°–90°, 90°–120°, 120°–150°, 150°–180°) ANOVA. No three-way interaction emerged, $F(5,155) = 0.65, p > .1$, which suggests that RT patterns were similar for the MRT and PRT. Note that three of the 768 cells in this analysis were empty as a result of participant error and replaced with averages of the same cell across participants. A two-way trial type × initial angular disparity bin interaction emerged, $F(5,155) = 16.6, p < .001, \eta_p^2 = .349$, which reflects that same-trial RTs linearly increased with initial angular disparity but different-trial RTs did not vary. This analysis further revealed main effects of task and trial type. RTs for PRT trials were slower than RTs for MRT trials, $F(1,31) = 59.62, p < .001, \eta_p^2 = .658$, and slower for different than for same trials, $F(1,31) = 40.71, p < .001, \eta_p^2 = .568$. Figure 3 depicts the ADEs and shows that RT patterns were similar for both tasks.

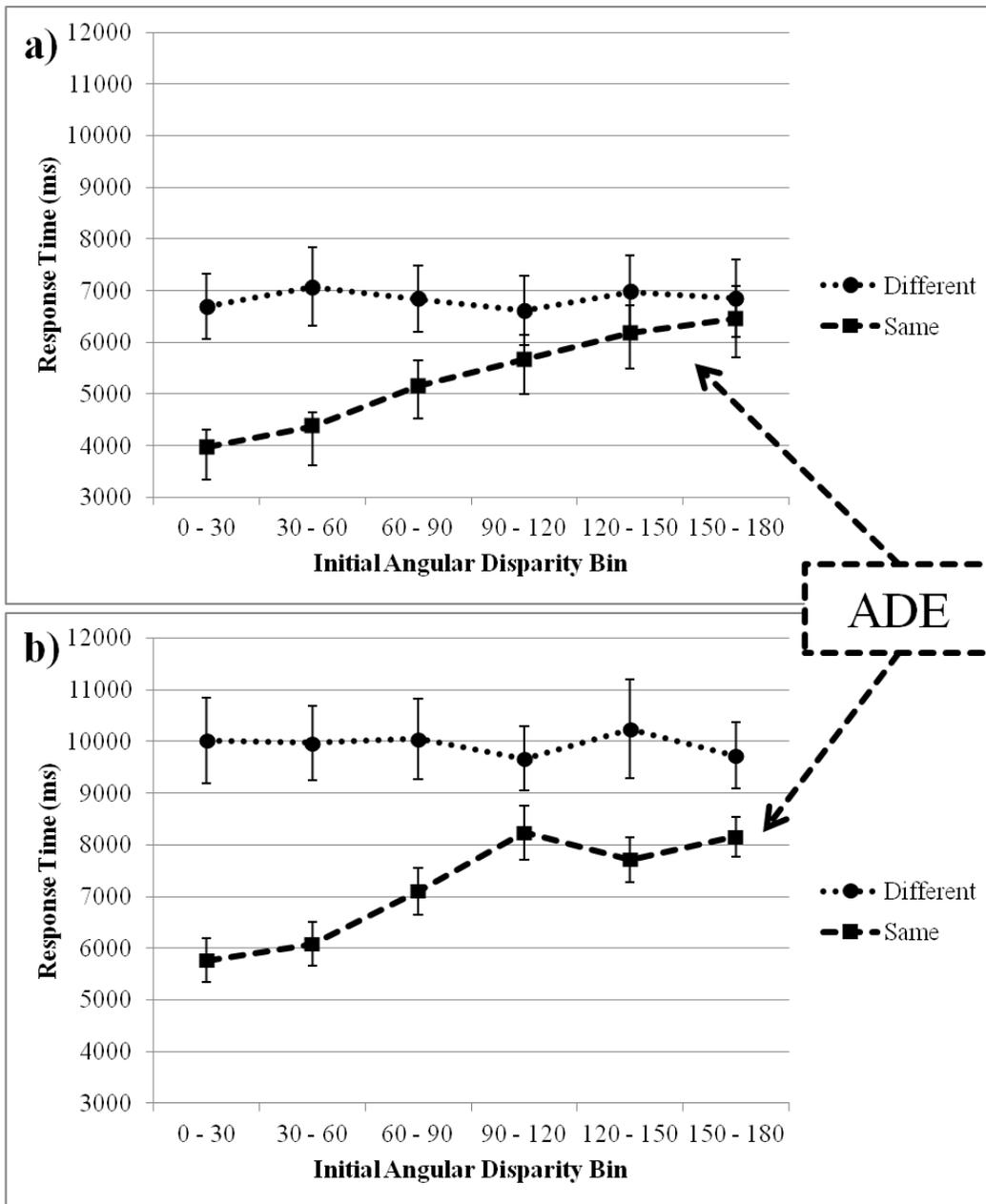


Figure 3. Experiment 1 mean RT as a function of initial-angular-disparity bin and trial type for the MRT (a) and PRT (b). Error bars show standard errors. Used with author permission from Gardony et al., 2014.

The same ANOVA used to examine RTs was used to investigate error rates. This analysis yielded similar findings, with no three-way interaction, $F_{GG}(3.83, 118.6) = 1.09, p > .1$. For some trials, a two-way trial type \times initial angular disparity bin interaction emerged, $F(5, 155) = 8.01, p < .001, \eta_p^2 = .205$, which reflects a positive linear relationship between initial angular disparity and error rate. For different trials, error rates did not vary with initial angular disparity. A main effect of task was also observed. PRT error rates were lower than the MRT, $F(1, 31) = 111.97, p < .001, \eta_p^2 = .783$. In contrast to the RT results, no trial type effect for error rates was observed, $F(1, 31) = 0.31, p > .1$. Figure 4 depicts the observed ADEs and shows that error rate patterns for the MRT and PRT were similar. Taken together, the RT and error rate data demonstrated a speed/accuracy trade-off. MRT responses were faster but less accurate than the PRT.

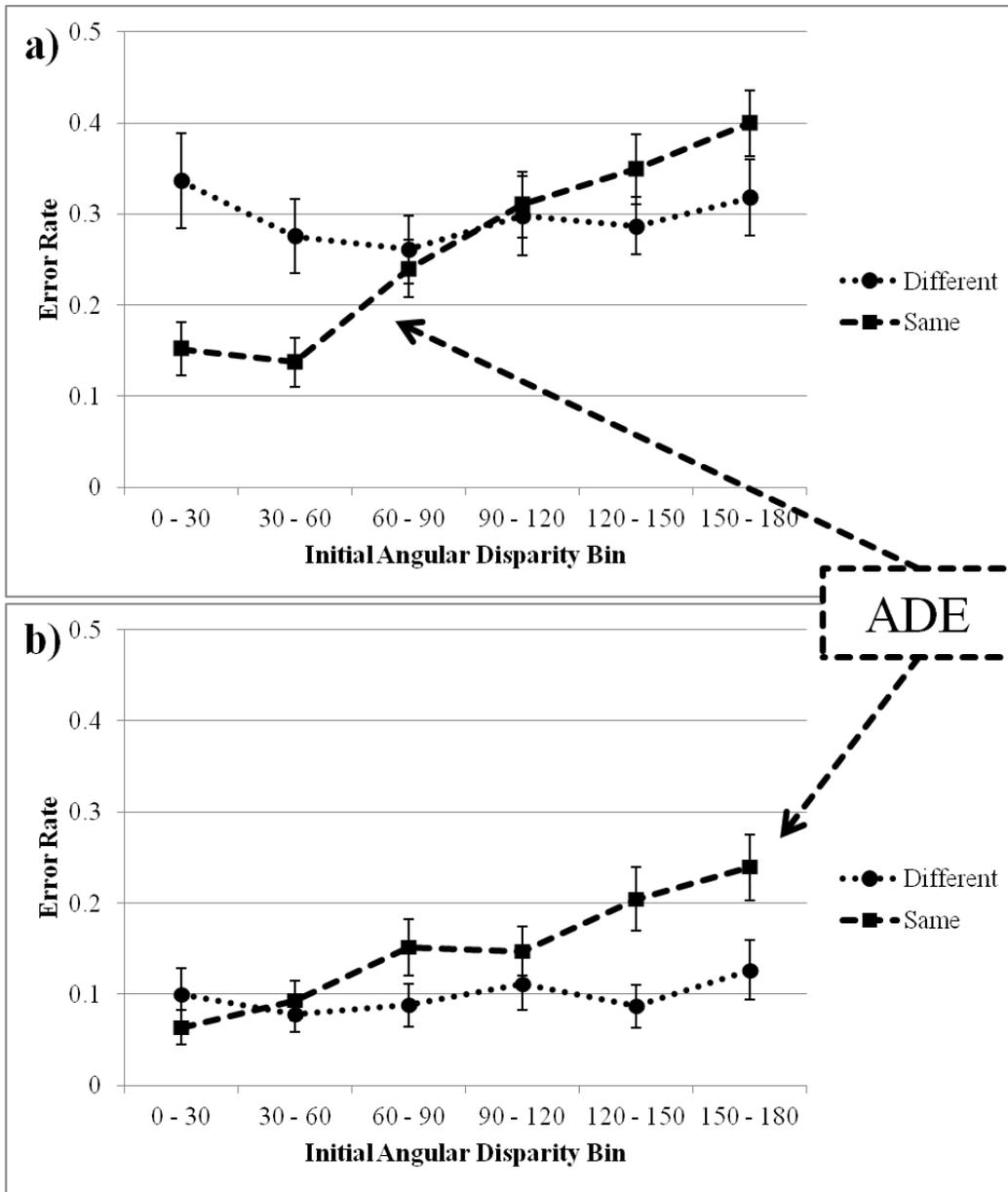


Figure 4. Experiment 1 mean error rate as a function of initial-angular-disparity bin and trial type for the MRT (a) and PRT (b). Error bars show standard errors. Used with author permission from Gardony et al., 2014.

We next examined continuous real-time angular disparity between the SM figure pairs in the PRT. Data varied between trials (trials with longer RTs had more data). To address this, we first normalized the data into 100 samples using linear interpolation. Second, to discretize the continuous time variable, we created a time factor by dividing each trial into interpolated time quartiles (Sample 1–25, 26–50, 51–75, 76–100). Third, we divided trials by initial angular disparity (30° bins) as before. We then conducted a 4 (time quartile) × 6 (initial angular disparity bin) × 2 (trial type) ANOVA, which yielded a three-way interaction, $F(15,465) = 5.99, p < .001, \eta_p^2 = .162$. Figure 5 depicts the continuous physical rotation data underlying this interaction. Rotation initiating from varying initial angular disparities converged to stable and distinct comparatives. Averaging angular disparity at sample 100 (angular disparity at response) demonstrated that same-trial rotation converged to 49°, whereas different-trial rotation converged to 113°. In neither case did rotation achieve a match between figures (i.e., 0°).

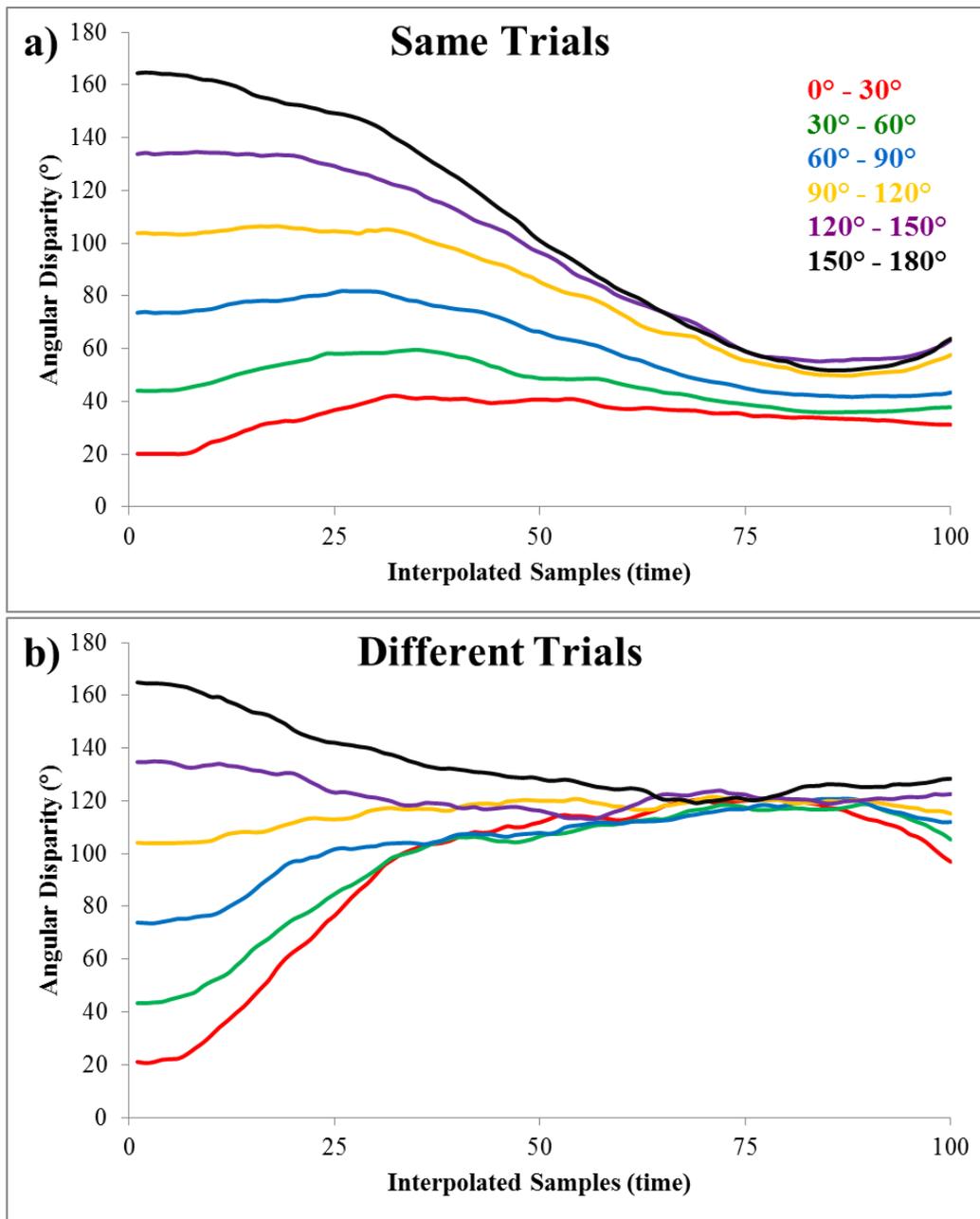


Figure 5. Experiment 1 fine-grain angular disparity dynamics for correct responses in the PRT as a function of time quartile and initial angular disparity bin. Results are shown separately for same (a) and different (b) trials. Used with author permission from Gardony et al., 2014.

Finally, we examined how stimuli features relate to the speed/accuracy trade-off. One influential theory posits that mental rotation involves three stages: search, transformation and comparison, and confirmation (Just & Carpenter, 1976). The time-intensive transformation and comparison stage involves switching gaze between SM figure pairs' exterior "arms" (see Figure 6). Thus, figures' arm characteristics may influence RTs. We devised a dichotomous factor, *symmetry*, coding figures symmetric if the exterior arms had an equal number of blocks and asymmetric if they did not. We also devised a dichotomous factor, *arm weighting*. Figures in which the majority of blocks were contained in their arms (six or more) were coded as having high arm weighting, and figures with five or fewer blocks were coded as having low arm weighting. Figure 6 presents example figures depicting these factors.

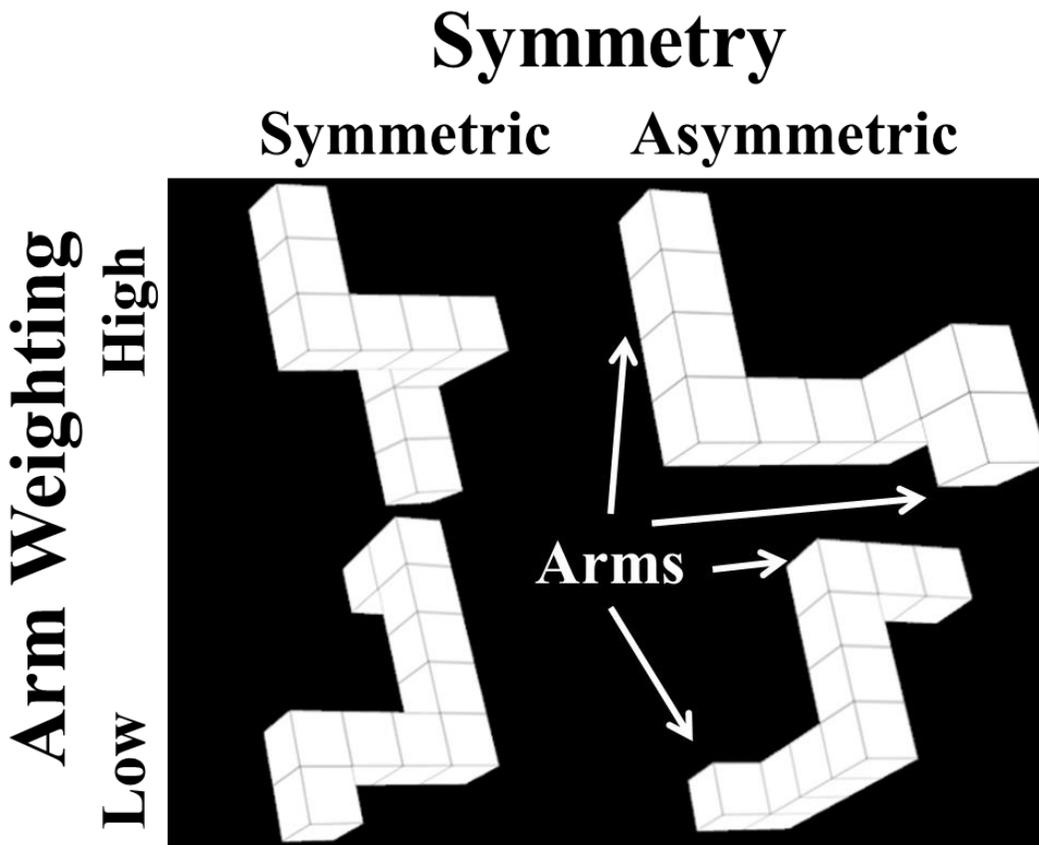


Figure 6. Examples from Experiment 1 of SM figures with differing symmetry and arm weighting. Figures were considered symmetric if their exterior arms had an equal number of blocks and asymmetric if they did not. Figures in which the majority of blocks were contained in their arms were coded as having high arm weighting; otherwise, they were coded as having low arm weighting. Used with author permission from Gardony et al., 2014.

We submitted RT data for same and different trials to a 2 (task: MRT, PRT) × 2 (symmetry: symmetric, asymmetric) × 2 (arm weighting: high, low) ANOVA, which revealed a three-way interaction (see Figure 7), $F(1,31) = 9.45, p < .01, \eta_p^2 = .234$, as well as main effects of symmetry, $F(1,31) = 17.23, p < .001, \eta_p^2 = .357$, and arm weighting, $F(1,31) = 24.49, p < .001, \eta_p^2 = .441$. RTs were slower for both symmetric (relative to asymmetric) figures and figures with high

(relative to low) arm weighting. Participants had the most difficulty responding to symmetric figures with high arm weighting in the PRT.

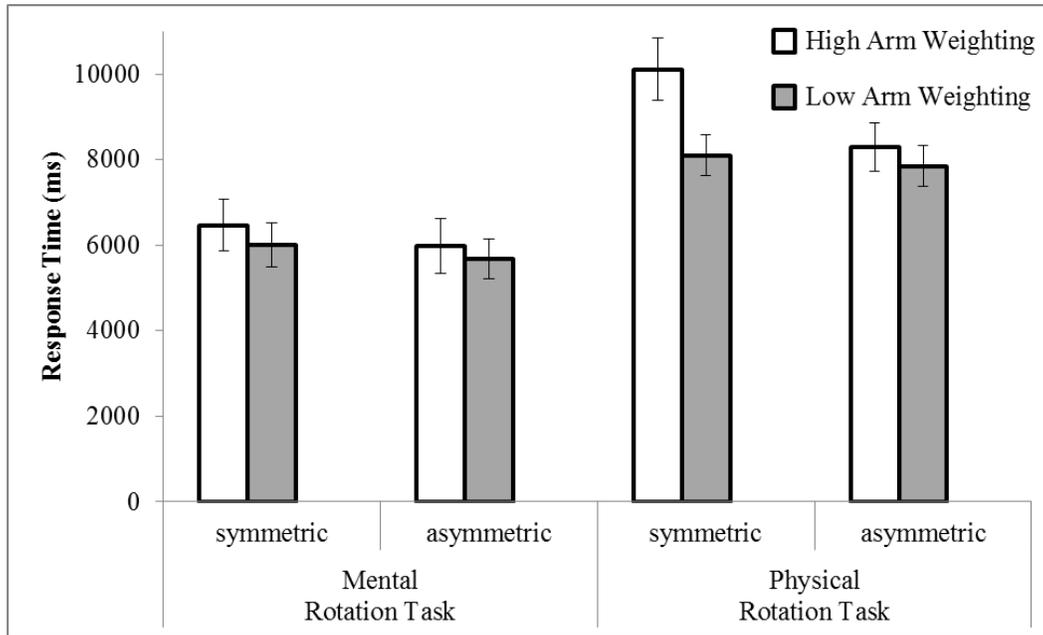


Figure 7. Experiment 1 mean RT for correctly answered same and different trials (collapsed) as a function of whether figures were symmetric or asymmetric and had high or low arm weighting. Results are shown separately for the MRT and PRT. Error bars show standard errors. Used with author permission from Gardony et al., 2014.

Individual Differences

To assess contributions of individual differences for each participant, we regressed RTs for correctly answered same trials with initial angular disparity, producing slopes of each participant's MRT and PRT ADE regression lines. We then regressed participants' individual difference measures with their slopes. Neither gender effects nor significant relationships between other individual differences and slopes emerged for either the MRT or PRT (all p 's > .1).

Discussion

In Experiment 1, we directly compared mental rotation and physical rotation to explore central assumptions in the mental rotation literature. The multi-strategy view posits that mental rotation is covert motor simulation. In line with this view, physical rotation should both behaviorally resemble and yield novel insight into mental rotation. Mental and physical rotation showed predicted similarities, yielding statistically indistinguishable ADEs. This similarity was tempered by the speed/accuracy trade-off, with mental rotation being faster but less accurate than physical rotation. The prediction that participants would physically rotate SM figures in same pairs to achieve a match was not supported. Rather, the continuous physical rotation data challenge the assumption that mental rotation involves rotating figures to achieve a match and also suggest that participants use markedly different strategies for same and different trials.

Are Mental Rotation and Physical Rotation Similar?

The observed ADEs and similar RT patterns for mental and physical rotation replicate the findings of Wohlschläger and Wohlschläger (1998), supporting their interpretations that mental rotation involves covert motor simulation and that mental and physical rotation are similar. However, those authors did not show a speed/accuracy trade-off. The items analysis provides a possible explanation. Figure 7 shows that PRT RTs for symmetric figures with high arm weighting are particularly lengthy. During physical rotation, participants necessarily use holistic mental rotation (Robertson & Palmer, 1983; Yuille & Steiger, 1982), because whole-figure movement corresponds with their manual

action. Leone, Taine, and Droulez (1993) hypothesized that participants mentally rotate objects about their principal planes. In the case of SM figures, this plane intersects the figure's center segment. Leone et al. (1993) suggested that a figure's principal plane is rotated holistically, whereas its arms are processed separately through an analytic search and confirmation process. According to this framework, symmetric figures with high arm weighting should be ill-suited for mental rotation, because they possess the majority of blocks in their arms and thus bias analytic strategies. Further, when figure arms have equal numbers of blocks, an analytic contrast heuristic cannot be used. However, the multi-strategy view posits the optimal MRT performance flexibly integrates both mental rotation and analytic strategies. This flexibility leads to task performance that is less sensitive to these stimuli features than the PRT which strongly biases mental rotation.

What Does Physical Rotation Reveal about Mental Rotation?

The results for physical rotation have two implications for mental rotation. First, participants did not rotate figures to achieve a match on either same or different trials. Strikingly, participants rotated figures on same trials with near-matching initial angular disparities ($\sim 20^\circ$) away from 0° , responding when rotation (49°) was further removed from a match. This challenges the assertion that mental rotation involves rotating objects to achieve a match, although it still supports rotation of analog mental images. What cognitive processes may underlie this novel behavioral observation? Seminal perception research demonstrated consistent preference for off-axis (3/4) canonical views of objects, likely because they display the most surfaces (Palmer, Rosch, & Chase, 1981). If

mental rotation involves phenomenologically depicting and manipulating an analog mental image, it follows that rotation converges to a similar off-axis canonical difference. Though this assumption is speculative, our results provide some evidence for it.

Second, the data for continuous physical rotation suggest that same and different judgments employ distinct strategies. Rotation converged to markedly different angular disparities on same (49°) and different (113°) trials. Participants rotated same figures to a canonical difference and different figures to a distinct view. Here, we define a canonical difference as an off-axis rotation that affords an optimized view for perception and comparison of stimuli features. The RT data provide further evidence for distinct strategies. RTs and error rates for both the MRT and PRT yielded ADEs for same trials, but no consistent relationship with angular disparity for different trials. Shepard and Metzler (1971) argued that analyzing different trials was impossible because different figures cannot be rotated to achieve a match. However, the continuous physical rotation data demonstrate consistent convergence suggesting that both same and different judgments involve rotation to a stable comparative.

Interim Conclusions

The ADE findings and similar response patterns for mental and physical rotation suggest shared processes, supporting the first claim of the multi-strategy view. Experiment 1 also yielded evidence for the strategy-integrative nature of the MRT (claim 2). Stimuli features, such as arm weighting and symmetry, influenced MRT and PRT performance differently. These differences likely stem

from different *strategy profiles* of the two tasks. While the PRT strongly biases holistic mental rotation, the MRT flexibly integrates both mental rotation and analytic strategies. Most importantly, the physical rotation data suggest reconsideration of a long-held assumption in the mental rotation literature. Mental rotation does not involve rotation of an analogous percept to a match but rather to an off-axis orientation.

Motivations for Experiment 2

It is important to note that the evidence provided by Experiment 1 for the multi-strategy view is indirect. One clear limitation is that the PRT involves physical rotation of stimuli with simultaneous, vivid *visual feedback*. Participants saw the virtual SM figures rotate onscreen in real-time, yoked to manual sensor rotation. This presents a potential problem. Observed physical rotation behavior may be task-specific and only reflect how individuals perform when manipulating a visually-experienced object rather than when mentally rotating an imagery-experienced percept. Consistent with this view, physical rotation may reflect mental rotation only in cases where individuals possess vivid mental imagery. Such individuals may mentally rotate vivid analogous percepts “in their mind’s eye” similar to physical rotation of figures in the PRT. Vivid visual feedback, whether internally generated or externally present, may drive the unique results observed in Experiment 1. Yet, vividness of mental imagery varies within the general population (Cui, Jeter, Yang, Montague, & Eagleman, 2007). Thus physical rotation may reflect mental rotation processing only for a subset of the population.

Another limitation of Experiment 1 concerns strategy profiles in the MRT. As reviewed above, the multi-strategy view posits that the MRT flexibly integrates both mental rotation and analytic strategies and that strategy use varies on a trial-by-trial basis due to several internal and external factors. Experiment 1's items analysis provides some support for the multi-strategy view but this support is constrained because individual trials were averaged within angular disparity bins prior to analysis. This practice obfuscated potential trial-by-trial variation in strategy use. Moving forward, it is important to scrutinize individual trials in order to better understand dynamic strategy use in the MRT.

EXPERIMENT 2

Introduction

The multi-strategy view of mental rotation posits that optimal performance in the MRT involves flexibly integrating different cognitive strategies. Among these include mental rotation, where individuals mentally rotate analogous mental percepts by mentally simulating motor rotation, and an analytic strategy, where individuals use non-spatial, orientation-independent strategies, such as visual comparison of key object features. This multi-strategy nature is not unique to the MRT. Rather, these two strategies are generally applied in a range of spatial tasks (Hegarty, 2010). As such, it is important to characterize and understand the factors that influence *strategy profiles* in the MRT. Doing so can inform domain-general processes and have real world implications across a variety of domains (Taylor & Brunyé, 2013). For example, mental rotation ability is correlated with success in science, technology, engineering, and mathematics (STEM; Uttal,

Miller, & Newcombe, 2013). Thus, better understanding of cognitive strategies that contribute to MRT performance may inform current and future approaches to STEM education.

In this regard, the classic MRT has a major limitation; it is not strategy-transparent. The linear RT function (ADE), which is the behavioral hallmark of mental rotation, is not able to distinguish between different cognitive strategies used in the MRT. Indeed, the consistency in which the ADE is observed in mental rotation research has led many researchers to assume the MRT solely engages mental rotation. Yet, as reviewed above, many factors influence MRT strategy profiles. Perhaps the most important of these is task difficulty, which is operationalized as the angular disparity between SM figure pairs. Nearly all mental rotation experiments manipulate task difficulty to yield ADEs. Yet, research suggests that mental rotation is biased for easy trials while analytic strategies are biased for difficult trials (Cochran & Wheatley, 1989; Lohman & Kyllonen, 1983). Given the ubiquity of task difficulty manipulations in the mental rotation literature, it is important to examine how task difficulty influences strategy profiles.

Experiment 2 investigates strategy profiles in the MRT by observing and quantitatively categorizing physical rotation data. As a first step, we conducted a direct replication of Experiment 1 to corroborate our unexpected findings, using the same task. Hereafter we refer to this task as the physical rotation task with visual feedback (PRT_{VF}). Then, we created a novel task by modifying the PRT_{VF} so that participants *did not receive onscreen visual feedback* (i.e. the onscreen

figures remain static) when they manipulated the handheld sensor. For this physical rotation task without visual feedback (PRT_{NVF}), we instructed participants to mentally rotate the onscreen figures and to simultaneously manually rotate the sensor in the same direction as their mental rotation (i.e. “mirror” their mental rotation). The PRT_{NVF} allowed us to both remove the confounding variable of visual feedback from the PRT_{VF} and compare the old task with the new. Lastly, we used the PRT_{NVF} to infer cognitive strategies in the MRT and to examine the influence of task difficulty on MRT strategy profiles.

We first predicted that the key findings from Experiment 1 would replicate. We predicted the PRT_{VF} would yield an ADE and the real-time rotation data would not converge to a match, but to an off-axis orientation. By confirming Experiment 1’s findings, we would establish a consistent behavioral pattern associated with physical rotation of the SM figures. Then we could use this pattern to help categorize physical rotation behavior in the PRT_{NVF} . If, in the PRT_{NVF} , participants rotate the sensor in similar fashion to Experiment 1 it would suggest mental rotation was used. In this case, even though participants did not see the onscreen figures move, their physical rotation mirroring their mental rotation processes would resemble the stable behavioral pattern seen when the figures are manually rotated. In other words, their inferred mental rotation resembles actual physical rotation. In contrast, if participants rotated the sensor in a different pattern this would suggest use of a distinct cognitive strategy.

Based on this logic, we predicted that participants’ physical rotation data in the PRT_{NVF} would reflect different biasing of MRT strategies based on task

difficulty. Consistent with the multi-strategy view, physical rotation data in this task *should not* resemble those in Experiment 1 because mental rotation is not consistently used in the MRT. Instead, we predicted that for easy trials participants would manipulate the sensor similarly to Experiment 1, suggesting mental rotation was used. In contrast, for difficult trials, we predicted physical rotation data would yield a pattern distinct from Experiment 1. This finding would suggest use of distinct analytic strategies. This predicted interaction would be consistent with previous literature on strategy biasing in spatial tasks (Cochran & Wheatley, 1989; Lohman & Kyllonen, 1983).

In addition, we predicted that use of mental rotation vs. analytic strategies would vary in the PRT_{NVF} due to individual differences. Recall that in Experiment 1's PRT, participants received vivid visual feedback during physical rotation. It follows that individuals with high self-reported mental imagery vividness may experience similar vivid feedback when they mentally rotate in the PRT_{NVF} . As a result, their physical rotation data may more closely resemble Experiment 1's data, suggesting a preference for mental rotation. Other individual differences may also play a role. Gender differences favoring males are frequently reported in the mental rotation literature (Linn & Petersen, 1985; Miller & Halpern, 2014; Voyer et al., 1995) but recent research suggests that males and females perform equivalently in tasks that recruit mental rotation (Alexander & Evardone, 2008; Christova et al., 2008). Thus, the male MRT advantage may stem from a bias to recruit distinct analytic strategies when such strategies seem optimal. In line with this view, in the present experiment, we would expect males to bias analytic

strategies for difficult trials more so than females. In contrast, females may generally bias mental rotation, a strategy profile that would disadvantage them for difficult trials. It is important to note, however, that computer and video game experience substantially mediate gender effects in MRT performance (Terlecki & Newcombe, 2005) and that video game training can reduce gender effects (Feng, Spence, & Pratt, 2007). As such, differences in video game experience may yield effects similar to gender differences. Lastly, recent theory suggests that a key component of spatial intelligence is the ability to flexibly bias mental simulation and analytic forms of thinking (Hegarty, 2010). In line with this view, high spatial ability individuals should trade off more flexibly between mental rotation and analytic strategies.

Method

Participants

Sixty-four Tufts University undergraduates (mean age = 20.6 years; 32 male, 32 female) participated for monetary compensation.

Materials

Figures and Stimuli Presentation. Experiment 2 used the same apparatus as Experiment 1.

Questionnaires. We added new questionnaires and removed others in Experiment 2. We added a commonly used handedness inventory (Oldfield, 1971) and two self-report questionnaires of mental imagery vividness, the VVIQ-2 (Marks, 1995) and the Shapes Questionnaire (Dean & Morris, 2003). We retained the video game experience questionnaire (Boot et al., 2008), the Santa Barbara

Sense of Direction Scale (SBSODS; Hegarty et al., 2002), and the English FRS questionnaire on spatial strategies (FRS; Münzer & Hölscher, 2011) from Experiment 1. Table 2 presents the summary statistics of questionnaire responses for Experiment 2's sample.

Table 2. Experiment 2 individual difference measures.

Individual Difference	Questionnaire/Assessment	Statistics & Interpretation
Spatial ability	Santa Barbara Sense of Direction Scale (Hegarty, et al., 2002)	Moderate sense of direction $M = 4.4$, scale: 1 - 7
Spatial self-confidence, survey strategy, and knowledge of cardinal directions	English FRS questionnaire on spatial strategies (Münzer & Hölscher, 2011)	Moderate self-confidence in spatial abilities $M = 4.4$, scale: 1 - 7 Moderate preference for survey strategies $M = 4.1$, scale: 1 - 7 Low knowledge of cardinal directions $M = 2.3$, scale: 1 - 7
Video game experience	Video game experience questionnaire (Boot et al., 2008)	Moderate video game frequency $M = 1.4$ hours per week
Handedness	Edinburgh Handedness Inventory (Oldfield, 1971)	Large right hand bias $M = 1.4$ scale -2 (LH) - +2 (RH) 61 / 64 participants self-reported right handed
Vividness of Mental Imagery	VVIQ-2 (Marks, 1995) --- Shapes Questionnaire (Dean & Morris, 2003)	Moderate-high mental imagery vividness $M = 3.6$, scale 1 – 5 --- Moderate-high ease of mental imagery formation $M = 6.2$, scale 1 – 9 Moderate pictorial instability of mental imagery $M = 4.5$, scale 1 – 9 Moderate ease of mental imagery rotation $M = 5.8$, scale 1 – 9 Moderate relative size of mental imagery $M = 5.2$, scale 1 – 9

Procedure

Participants were randomly assigned to one of two conditions: the physical rotation task with visual feedback (PRT_{VF}) or without (PRT_{NVF}). The PRT_{VF} was identical to Experiment 1's PRT. As before, participants made parity judgments of rotated SM figure pairs while simultaneously rotating one designated response figure using the bimanually held sensor. In contrast, the PRT_{NVF} had different experimental instructions and did not provide visual feedback. Here participants were instructed to rotate the sensor to *mirror* their mental rotation. For example, if on a particular trial the participant was mentally rotating the response figure clockwise then they would also physically rotate the sensor clockwise. During sensor manipulation the figures remained *static* onscreen, like a typical MRT trial. However, we recorded sensor rotation and interpreted it as if the response figure's orientation was coupled with the sensor (resolution: 50 Hz), as in the PRT_{VF} . All other aspects of the PRT_{NVF} were identical to the PRT_{VF} .

Participants first completed the MRT, preceded by five practice trials that used figures distinct from those in the main experiment. Then participants completed either the PRT_{VF} or PRT_{NVF} , each preceded by five practice trials. As in Experiment 1, PRT_{VF} participants completed five practice trials in which they practiced rotating the response figure with the sensor. In the PRT_{NVF} participants first completed three identical practice trials in which they also practiced rotating the onscreen response figure. This demonstrated that sensor rotation corresponded one-to-one with figure rotation. Then participants completed two remaining practice trials in which the figures remained static with sensor rotation. This

demonstrated the idea of mirroring mental rotation. The main experiment task followed. As in Experiment 1, it consisted of three trial blocks, each containing 15 same and 15 different trials in which the figures were randomly selected (without replacement) from the stimulus set. Trials were separated by a screen instructing participants to return the sensor to the starting position. Error rates, RTs (time-locked to voice onset), and real-time angular disparities (50 Hz) were recorded. Upon completion of the main task, participants completed the questionnaires and then were debriefed and compensated.

Results

Experiment 2 served two aims. First we sought to replicate the key findings from Experiment 1 in the PRT_{VF}. These key findings were 1) observation of statistically-indistinguishable ADEs for the MRT and PRT_{VF} and 2) physical rotation convergence to an off-axis orientation. Second we sought to explore dynamic strategy use in the PRT_{NVF}. We address these two aims in turn.

Aim 1: Do the main findings from Experiment 1 replicate?

We conducted the following analyses on data from participants in the PRT_{VF} condition ($n = 32$). We first examined correct responses to the MRT and PRT_{VF} for the presence of an ADE. As in Experiment 1, for each task and participant we correlated the initial angular disparities between same figure pairs and RTs. This analysis revealed ADEs in both the MRT and PRT_{VF}. Pearson correlation coefficients (MRT: mean $r = .36$, PRT_{VF}: mean $r = .28$) differed significantly from zero — MRT: $t(31) = 11.21, p < .001$, PRT_{VF}: $t(31) = 8.53, p <$

.001, and a paired t test comparing the correlation sets was not significant, $t(31) = 1.88$, $p = .07$, suggesting that ADEs were similar between tasks.

We next examined continuous real-time angular disparity between the SM figure pairs in the PRT_{VF}. We employed repeated measures analyses of variance (ANOVAs), with Greenhouse-Geisser correction in the case of sphericity violations (Geisser & Greenhouse, 1958), denoted by F_{GG} . Data varied between trials and we applied the same normalizing procedure from Experiment 1 and divided trials into four time quartiles. We then conducted a 4 (time quartile) \times 6 (initial angular disparity bin) \times 2 (trial type) ANOVA, which yielded a three-way interaction, $F_{GG}(8.12, 251.58) = 3.53$, $p = .001$, $\eta_p^2 = .102$. Figure 8 depicts the continuous physical rotation data underlying this interaction. The pattern of data strongly resembled that found in Experiment 1. Rotation initiating from varying initial angular disparities converged to stable and distinct comparatives.

Averaging angular disparity at sample 100 (angular disparity at response) demonstrated that same-trial rotation converged to 55° (Exp 1: 49°), whereas different-trial rotation converged to 110° (Exp 1: 113°). In neither case did rotation achieve a match between figures (i.e., 0°). We confirmed that the data patterns did not statistically differ by conducting the three-way ANOVA above and including experiment (levels: 1, 2) as a between-participants factor. The critical four-way interaction was not significant, $F_{GG}(8.96, 555.7) = 1.26$, $p > .1$.

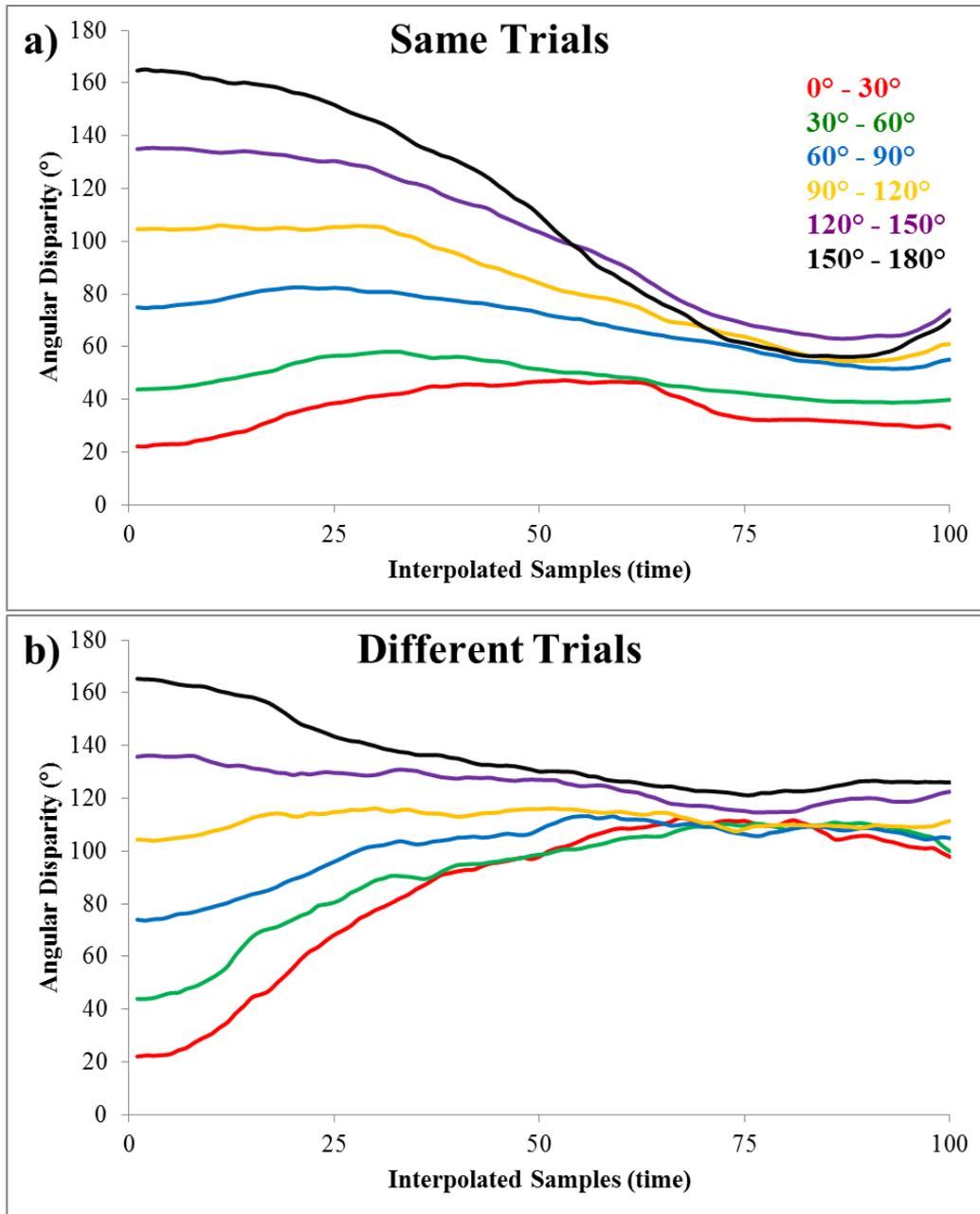


Figure 8. Experiment 2 fine-grain angular disparity dynamics for correct responses during the PRT_{VF} as a function of time quartile and initial angular disparity bin. Results are shown separately for same (a) and different (b) trials.

Aim 2: Inferring Strategies from the PRT_{NVF}

We conducted the following analyses on PRT_{NVF} data ($n = 32$). We first examined whether Experiment 1's key findings were also present in the PRT_{NVF}

data. We scrutinized correct responses to same trials (i.e. “hits”) in the MRT and PRT_{NVF} for the presence of an ADE using the same procedure described above. This analysis revealed ADEs in both the MRT and PRT_{NVF} . Pearson correlation coefficients (MRT: mean $r = .29$, PRT_{NVF} : mean $r = .48$) differed significantly from zero — MRT: $t(31) = 7.05$ $p < .001$, PRT_{NVF} : $t(31) = 20.34$, $p < .001$. In contrast to Experiment 1, a paired t test revealed that the ADE correlation coefficients for the PRT_{NVF} were greater than the MRT, $t(31) = 4.14$, $p < .001$.

We next examined continuous real-time angular disparity between the SM figure pairs in the PRT_{NVF} . We applied our normalization procedure and conducted a 4 (time quartile) \times 6 (initial angular disparity bin) \times 2 (trial type) ANOVA, which yielded a three-way interaction, $F_{GG}(7.7, 238.62) = 2$, $p = .05$, $\eta_p^2 = .06$. Figure 9 depicts the continuous physical rotation data underlying this interaction. In contrast to the PRT_{VF} , PRT_{NVF} data only somewhat resembled that found in Experiment 1 with reduced convergence overall. Rotation neither converged to distinct stable comparatives nor to a match between figures (i.e., 0°). Further, we confirmed that the data patterns statistically differed from Experiment 1 by conducting the same 4-way ANOVA above that included experiment as a between-participants factor. The critical four-way interaction was significant, $F_{GG}(8.22, 509.87) = 4.05$, $p < .001$, $\eta_p^2 = .06$.

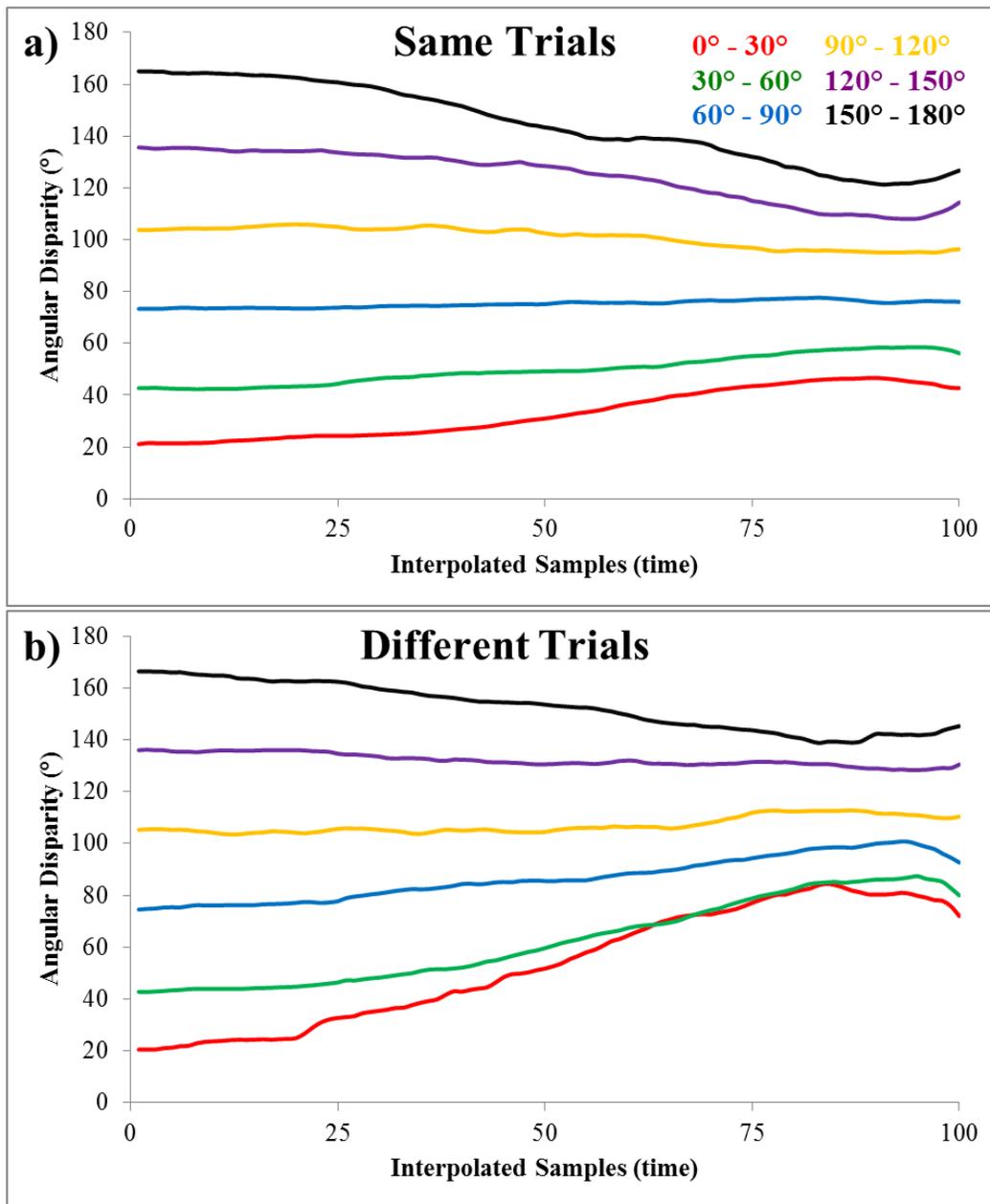


Figure 9. Experiment 2 fine-grain angular disparity dynamics for correct responses during the PRT_{NVF} as a function of time quartile and initial angular disparity bin. Results are shown separately for same (a) and different (b) trials.

Data Mining Strategies from the PRT_{NVF}

The apparent differences between the PRT_{NVF} and PRT_{VF} physical rotation data suggest that the PRT_{NVF} involves more than just mental rotation.

Consequently, we scrutinized cognitive strategies in the PRT_{NVF} . In order to group trials into different strategies we first needed to quantitatively measure inter-trial similarity. Recall that each trial measures the angular disparity between SM figure pairs over time (i.e. a time series). Further, trial duration (i.e. the number of samples) varies between trials and depends on RT. Relatively fast RT trials have fewer samples while slower RT trials have more. In previous analyses, we addressed this aspect of our data by standardizing data length with linear interpolation prior to averaging. However, for strategy classification, this step was not necessary as existing data mining techniques can assess inter-trial similarity of non-standardized data.

Dynamic time warping (DTW; Berndt & Clifford, 1994) can measure the dissimilarity (or distance) between time series data of varying length. DTW works by stretching and compressing one time series along the time axis in order to map one or more elements of the series to those of another time series. The mathematical and algorithmic details of this procedure are outside the scope of this dissertation (but see Müller, 2007, chapter 2 for review). Given its utility in assessing similarity of length-varying time series data, we decided to use DTW to mine the PRT_{NVF} data. We then applied cluster analyses to the resulting distance matrices to extract latent strategies from the data. Specifically we used k-medoids cluster analysis (see Kaufman & Rousseeuw, 1990 for review), a preferable

technique for DTW distance (Niennattrakul & Ratanamahatana, 2007). We used MATLAB implementations of DTW and k-medoids. Appendix C provides details of these implementations.

Cluster Analysis. As a first step we selected correct-response “same” trials (i.e. “hits”). Prior to analysis we filtered out trials that possessed fewer than five samples of data. On these trials, errant vocalizations (e.g. coughs, sniffles, etc.) led to immediate and unintended responses. We also removed trials in which participants failed to adequately reset the sensor to its starting position. For these trials, the initial angular disparity and the first sample of rotational data differed by more than 15 degrees. Ideally, this difference should be close to zero plus or minus a few degrees due to human error. This procedure removed 76 (6.4%) of the 1179 trials (1103 remaining). We then divided the trials into six initial angular disparity bins, as before. For brevity we hereafter refer to these as “bins.” Next, we computed intra-trial resemblance within each bin in pairwise fashion using DTW, yielding six distance matrices. Lastly, we conducted k-medoids cluster analysis on these matrices.

K-medoids, like the well-known k-means technique, requires the number of clusters, k , to be specified prior to analysis. Researchers may set k based on a priori assumptions regarding the number of clusters in the dataset. In our case, we sought to examine the presence of mental rotation and analytic strategies in the data but the number of possible strategies was unknown. Thus, we conducted exploratory analyses to determine the appropriate value of k for our data set. For each bin we conducted cluster analyses with k ranging from 1 to 7. We ran each

cluster analysis five times, selecting the analysis which yielded the lowest total cluster energy to avoid local-minima traps. Then to determine the appropriate value of k we employed the commonly used “elbow method” on the sum of squared error (SSE) of each cluster solution. SSE can be interpreted as the global error associated with a cluster solution. For our data, SSE is defined as the sum of the squared DTW distance of each trial to its cluster medoid. We computed seven SSEs (one for each value of k) for each bin. We then averaged the corresponding SSEs across bins and plotted the average SSEs. As depicted in Figure 10, the averaged SSE (error) decreases with increasing k , as expected. After $k = 3$, reduction in SSE slows producing an “elbow” in the graph. Consequently we selected $k = 3$ as the appropriate number of clusters for our data set.

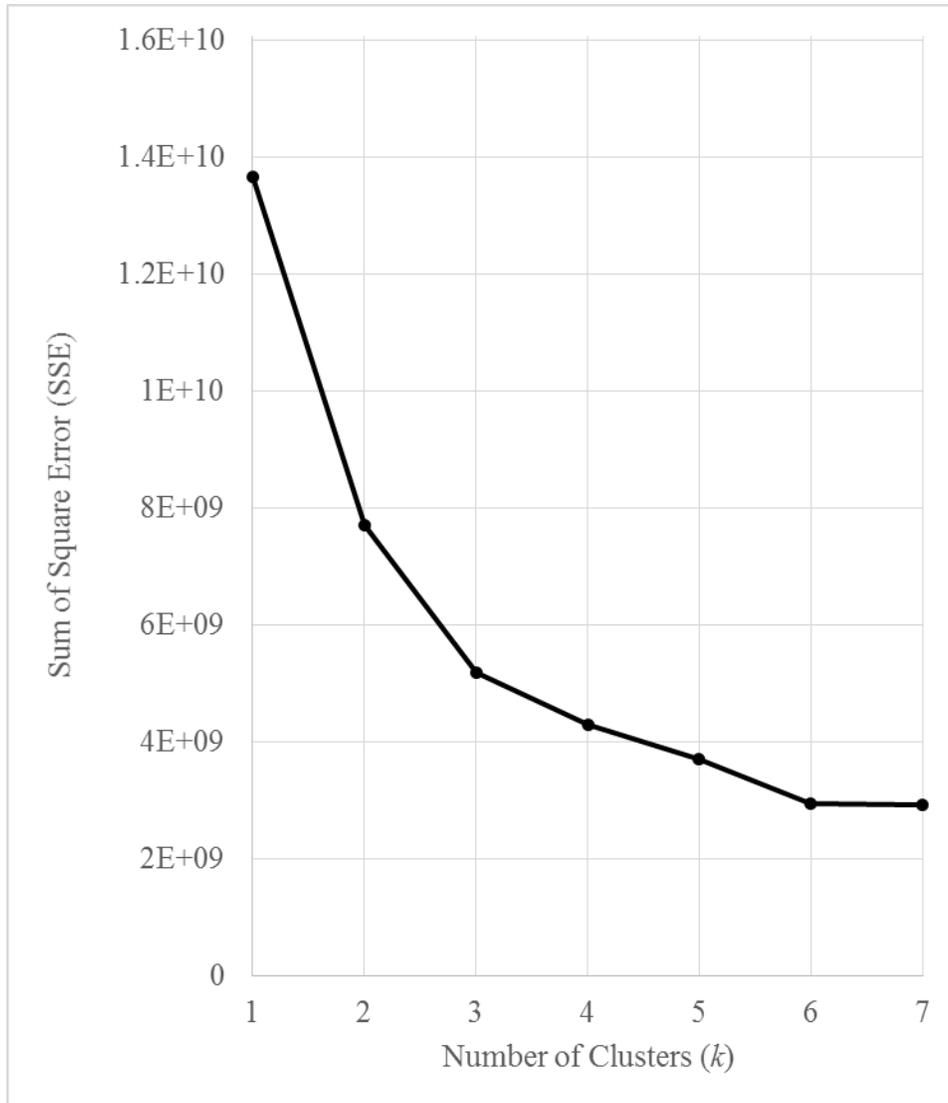


Figure 10. SSEs for candidate cluster solutions for Experiment 2’s PRT_{NVF} data.

We next quantitatively inspected the three extracted clusters in each bin to determine if they resembled the data from Experiment 1. Within each bin we computed similarity of each trial to the normalized averaged curves from Experiment 1 (see Figure 5a) using DTW. Then we averaged these similarities within clusters. For each bin, we selected the cluster with the greatest similarity and designated it as the motoric strategy because it best resembled the physical rotation data from Experiment 1. The remaining two clusters were designated

analytic strategies. Of these, one strategy appeared to be cognitively meaningful and reflected limited movement of the sensor (i.e. a “don’t move” strategy). To confirm this, we computed standard deviations of real-time angular disparity for each trial and averaged deviations within clusters. For each bin, we selected the cluster with the lowest mean standard deviation from the two remaining and designated it as the “don’t move” strategy. Lastly, we designated the last cluster as the high variability strategy, given its relatively high standard deviation.

To visually depict these strategies, as before, we normalized the data to 100 samples using linear interpolation and averaged the data within bin and cluster. Figure 11 depicts the motoric strategy and Figures 12a and 12b depict the analytic strategies. Visual examination of individual trials suggested that the motoric and “don’t move” strategies reflected consistent behavior. The motoric strategy resembled the physical rotation data from Experiment 1 and the “don’t move” strategy suggested limited sensor movement in favor of visual examination of the stimuli. In contrast the high variability strategy did not reflect a consistently applied strategy. Rather, this cluster appeared to contain highly variable trials that did not cleanly fit into either of the other clusters. As such, the averaged curves of this “strategy” (see Figure 12b) should be interpreted with caution.

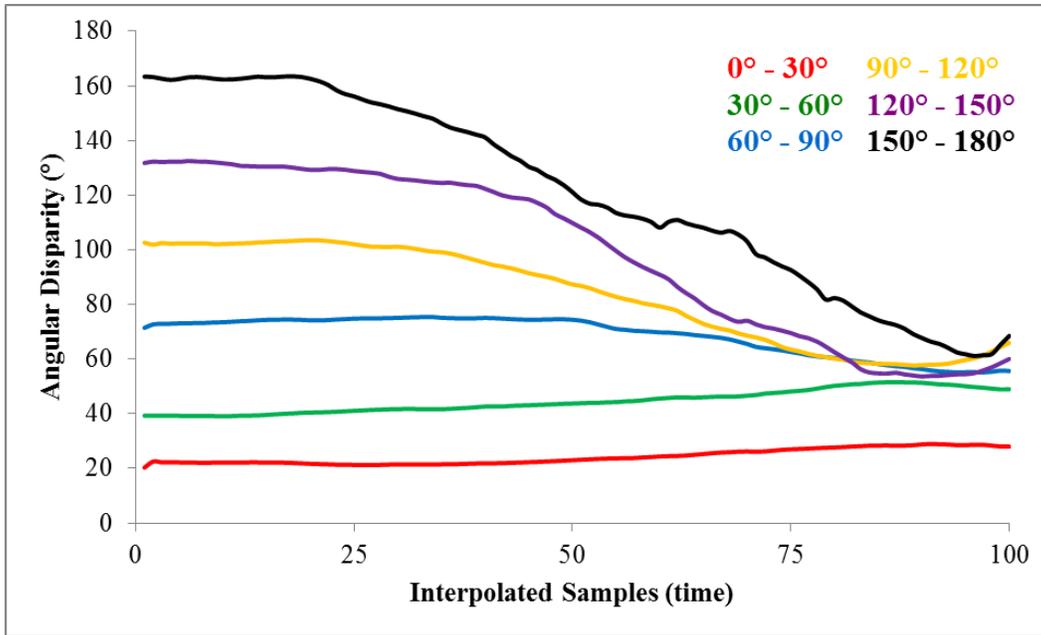


Figure 11. Experiment 2 fine-grain angular disparity dynamics of the motoric strategy in the PRT_{NVF} . Real-time angular disparity of hit trials are plotted as a function of time quartile and initial angular disparity bin.

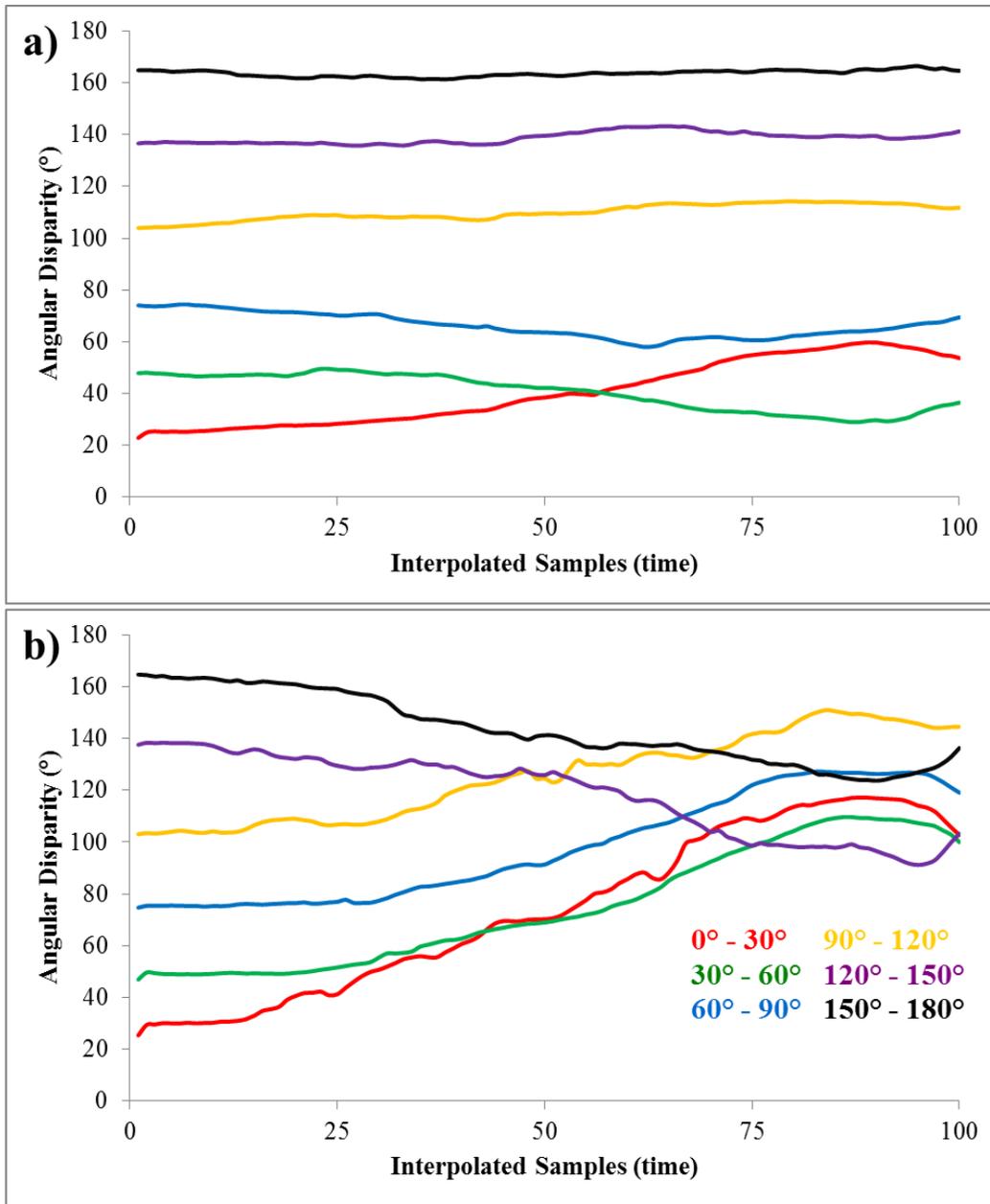


Figure 12. Experiment 2 fine-grain angular disparity dynamics of the analytic strategies in the PRT_{NVF} . The top panel (a) depicts the “stay same” strategy and the bottom panel (b) depicts the high variability strategy. Real-time angular disparity of hit trials are plotted as a function of time quartile and initial angular disparity bin.

Strategy Use and PRT_{NVT} Performance – Task Difficulty

Having separated the PRT_{NVT} data into different strategies, we next examined how strategy use and RT varied as a function of task difficulty. Here, we used initial angular disparity to operationalize task difficulty. Because the high variability strategy did not appear to be cognitively meaningful we omitted it from the following analyses and instead directly compared the motoric and “don’t move” strategies. This pared dataset contained 847 trials (23% trials removed).

Linear Mixed-Models. In the following analyses we employed linear-mixed models (LMMs) which offer key advantages over general linear model (GLM) approaches such as ANOVA or regression. LMMs are robust to missing data and are well-suited for data collected from repeated-measures designs (Krueger & Tian, 2004; West, Welch, & Galecki, 2015). Importantly, LMMs include both fixed effect parameters, which are akin to predictors or independent variables in the GLM approach, as well as *random effects*, which model unobserved random variables such as nonlinear variation between participants or tested items in a dataset. We ran linear mixed-model analyses using R (R Development Core Team, 2014) and the lme4 package (Bates, Maechler, Bolker, & Walker, 2014). We visualized the models with effects plots generated with the effects package (Fox, 2003). For strategy use, we employed a binomial generalized linear mixed-model (GLMM) using lme4’s glmer function and conducted significance testing with likelihood ratio tests (LRTs) using R’s native anova function. For RT, we employed a linear mixed-model (LMM) using lme4’s lmer function and conducted significance testing with the lmerTest package

(Kuznetsova, Brockhoff, & Christensen, 2014), which provides F statistics, degrees of freedom estimated using the Satterthwaite approximation, and p -values.

Strategy Use. We first examined strategy use. We assigned a binary score to each trial based on the used strategy (motoric = 1, “don’t move” = 0). Then, using these scores, we conducted a mixed-effects logistic regression on strategy use as a function of initial angular disparity. We first entered the binary scores as the dependent variable in the GLMM. Then we entered grand-mean centered initial angular disparity as the sole fixed effect in the model. To determine the random effects structure we sequentially specified random intercepts for participant and item followed by random slopes for the by-participant and by-item effect of angular disparity. Following the addition of each random effect we conducted a LRT of the current model against the previous model. If this test was significant ($p < .05$) the effect was included in the random effects structure of the final model. As a result of this procedure, we included random angular disparity slopes and intercepts for participants in the model’s random effects, omitting item-related random effects. To test significance of the model’s sole fixed effect we obtained p -values with a LRT of the full model containing the fixed effect of interest against an alternative model without the effect.

This analysis revealed a main effect of initial angular disparity, $\chi^2(1) = 17.41, p < .001$. As shown in Figure 13, participants appeared to trade off between strategies, biasing the motoric strategy for low-difficulty (small angular disparity) trials and the “don’t move” strategy for high-difficulty (large angular

disparity) trials. In addition, participants biased the motoric strategy overall as indicated by the significant negative β coefficient for the model intercept (see Table 3). Applying an inverse-logit transform to this coefficient revealed that on average participants used the motoric strategy 56% of the time.

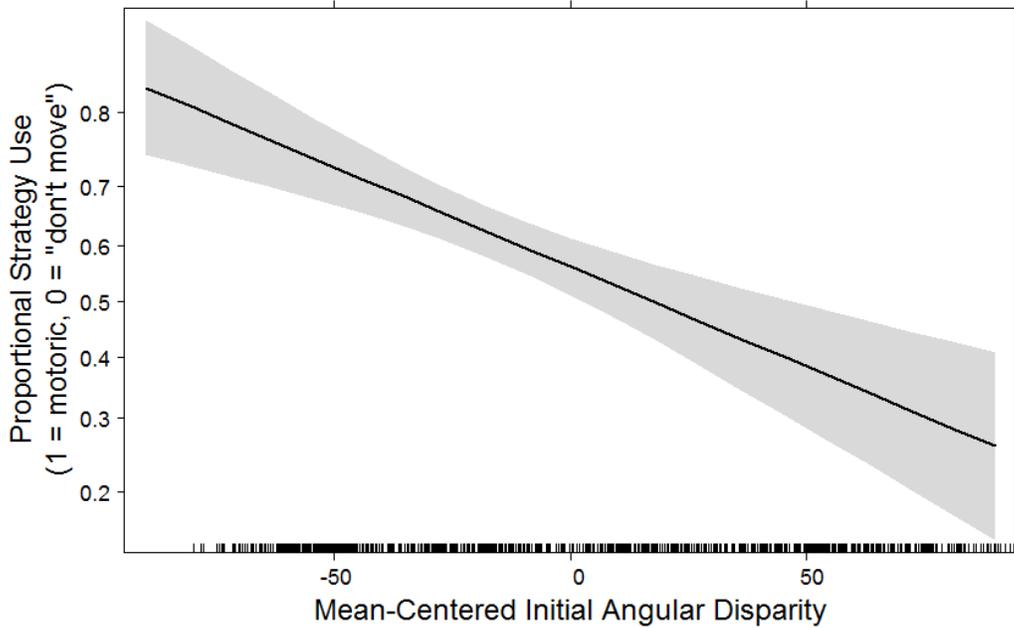


Figure 13. Experiment 2 effects display for the effect of initial angular disparity on strategy use in the PRT_{NVF} . Bands depict 95-percent pointwise confidence interval.

Table 3. Experiment 2 coefficient estimates (β), standard errors $SE(\beta)$, and associated Wald’s z-score ($=\beta/SE(\beta)$) for the generalized linear mixed-model predicting strategy use (motoric = 1, “don’t move” = 0) as a function of initial angular disparity.

	Coef. β	$SE(\beta)$	z
(Intercept)	2.55e-01	1.05e-01	2.42 *
grand-mean centered initial angular disparity	-1.45e-02	3.16e-03	-4.60 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Response Time (RT). We next examined how RT varied by strategy used and task difficulty. We first entered RT as the dependent variable in the LMM.

Then we entered grand-mean centered initial angular disparity, strategy used, and their interaction as fixed effects into the model. We determined the random effects structure of the model using the iterative procedure detailed above. As a result, we included random angular disparity slopes and intercepts for participants, omitting item-related random effects, as before. Initial visual inspection of residual scatter and Q-Q plots suggested heteroscedasticity and a positively skewed distribution that deviated from normality. To correct this we log-transformed RT prior to analysis. In addition, we assessed the model for multicollinearity by computing variance inflation factor (VIF) for each of the fixed effects in the model. VIF represents the proportion of variance in one predictor explained by all the other predictors in the model. $VIF > 4$ is a commonly used threshold for model multicollinearity and all of the fixed effects met this criterion (but see: O'Brien, 2007 for discussion of the limitations of such VIF "rules of thumb").

The analysis revealed a main effect of angular disparity, $F(1,101.39) = 237.69, p < .001$, reflecting the presence of an ADE. There was no main effect of strategy, $F(1,815.96) = 2.84, p = .09$. Importantly, the strategy x difficulty interaction was significant, $F(1,804.77) = 16.22, p < .001$. Follow-up Bonferroni-corrected LMMs within each strategy ($\alpha_{\text{critical}} = 0.025$) confirmed ADEs for both the motoric, $F(1,25.37) = 130.37, p < .001$, and "don't move" strategies, $F(1,20.46) = 49.15, p < .001$. As shown in Figure 14, RT was faster for the motoric strategy when difficulty was low. However, when difficulty was high, RT

was faster for the “don’t move” strategy. Table 4 presents the coefficients of the model.

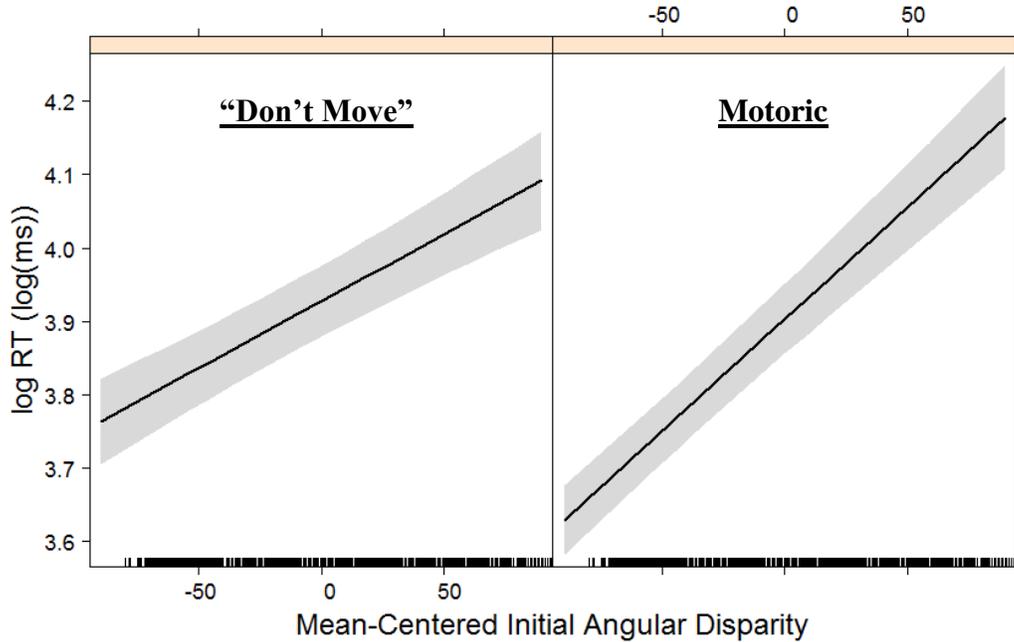


Figure 14. Experiment 2 effects display for the effect of initial angular disparity and strategy used on log RT in the PRT_{NVF}. 0 = “don’t move”, 1 = motoric. Bands depict 95-percent confidence interval.

Table 4. Experiment 2 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log(RT) as a function of initial angular disparity and strategy used (motoric = 1, “don’t move” = 0).

	Coef. β	SE(β)	df	t
(Intercept)	3.93e+00	2.48e-02	3.98e+01	158.64 **
grand-mean centered				
initial angular disparity	1.82e-03	2.27e-04	3.02e+02	8.05 ***
strategy used	-2.39e-02	1.42e-02	8.16e+02	-1.69 ⁺
grand-mean centered				
initial angular disparity x				
strategy used	1.22e-03	3.04e-04	8.05e+02	4.03 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Individual Differences - Strategy Use and PRT_{NVT} Performance

We next considered how inter-participant individual differences influenced strategy use and RT. We collected several individual difference measures (see Table 2), many of which were inter-correlated, a problem for the collinearity assumption of LMMs. To address this issue, we conducted principle components analysis (varimax rotation) on the measures, dummy coding gender (0 = male, 1 = female) and excluding handedness. This procedure yielded four factor scores. Table 5 presents the extracted components and their factor loadings and Table 6 presents the factor loadings for the components whose eigenvalues exceeded 1. Based on the factor loadings we interpreted each component as follows: imagery vividness / MR ability (1), spatial ability/self-confidence (2), gender / video game experience (3), and knowledge of cardinal directions (4). We then included these factor scores in the mixed-models from the previous analyses.

Table 5. Extracted components, eigenvalues, and % variance explained from principle components analysis of Experiment 2 individual difference measures (excluding handedness).

Component	Initial Eigenvalues	
	Total	% of Variance
1	4.03	36.68
2	2.13	19.34
3	1.22	11.10
4	1.07	9.71
5	0.59	5.40
6	0.51	4.65
7	0.45	4.13
8	0.32	2.89
9	0.31	2.82
10	0.21	1.90
11	0.15	1.37

Table 6. Factor loadings of extracted components from principle components analysis of Experiment 2 individual difference measures (excluding handedness). Maximally-loaded measures are bolded for each component and interpretations based of loadings are italicized.

Measure	Component 1 <i>Imagery Vividness/ MR Ability</i>	Component 2 <i>Spatial Ability/ Self-Confidence</i>	Component 3 <i>Gender/ VG Exp</i>	Component 4 <i>Knowledge of Cardinal Directions</i>
Gender	0.04	-0.25	-0.82	-0.27
SBSODS	0.03	0.88	0.20	0.13
FRS _{self_confidence}	0.23	0.87	0.03	0.07
FRS _{survey_strategy}	0.40	0.74	-0.06	0.06
FRS _{knowledge_cardinal}	0.16	0.29	0.27	0.81
Video game exp	0.14	-0.04	0.86	-0.01
VVIQ-2	0.62	0.37	0.24	-0.47
Shapes _{ease_formation}	0.82	0.10	-0.31	0.02
Shapes _{pict_instability}	-0.76	-0.21	-0.11	-0.14
Shapes _{ease_rotation}	0.78	0.24	0.28	0.10
Shapes _{relative_size}	0.53	-0.01	-0.50	0.43

Strategy Use. To ascertain the influence of individual differences on strategy use we reused the previous binomial GLMM predicting strategy use. As additional fixed effects, we entered each factor score as main effects as well as interactions with angular disparity. We did not include interactions between the factor scores. VIF was < 4 for all of the fixed effects in each model. As before, we determined the random effects structure for the model using our iterative procedure and consequently included random intercepts for participants and items. For each factor score we obtained p -values with LRTs of the full model containing the effect of interest against an alternative model without it. This analysis revealed a main effect of gender / video game experience, $\chi^2(1) = 5.96, p = .01$. High video game experience participants biased the motoric strategy more than low. It is also important to note that the factor loadings (see Table 6) and raw values for gender and video game experience were anti-correlated, $r(30) = -.53, p < .01$. Therefore, the effect also indicates that males biased the motoric strategy more frequently than females. No other individual difference main effects emerged (all p 's $> .1$).

We next examined factor score interactions with angular disparity. A spatial ability / self-confidence factor x angular disparity interaction emerged, $\chi^2(1) = 10.57, p = .001$. As shown in Figure 15, high-spatial participants traded off between strategies, biasing the motoric strategy for low-difficulty trials and the “don’t move” strategy for high-difficulty trials. In contrast, low-spatial participants minimally traded off between the motoric and the “don’t move”

strategies as difficulty increased. No other individual difference interactions emerged (all p 's > .1).

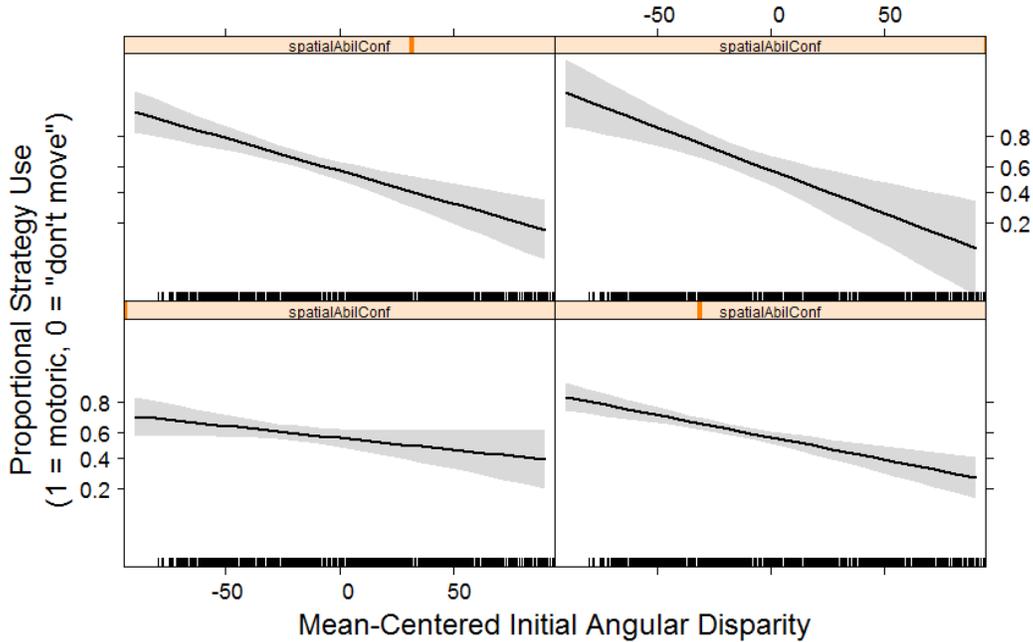


Figure 15. Experiment 2 effects display for the effect of the spatial ability / self-confidence factor and initial angular disparity on strategy use in the PRT_{NVF}. Bands depict 95-percent pointwise confidence interval.

Response Time (RT). To ascertain the influence of individual differences on RT we reused the previous LMM predicting log-transformed RT. As additional fixed effects, we entered each factor score as main effects as well as interactions with angular disparity and strategy used. We did not include interactions between the factor scores. VIF was < 4 for all of the fixed effects in each model. As before, we determined the random effects structure for the model using our iterative procedure and consequently included random intercepts for participants. The analysis revealed a trend-level main effect of the spatial ability / self-confidence factor, $F(1,26.67) = 3.83, p = .06$, with marginally faster RTs for high-spatial

participants than low. There was also a marginal spatial ability / self-confidence factor x angular disparity interaction, $F(1,809.08) = 3.63, p = .06$. As shown in Figure 16, increasing spatial ability / self-confidence was weakly associated with decreasing ADE slope. No other individual difference main effects or interactions emerged from this analysis (all p 's > .1).

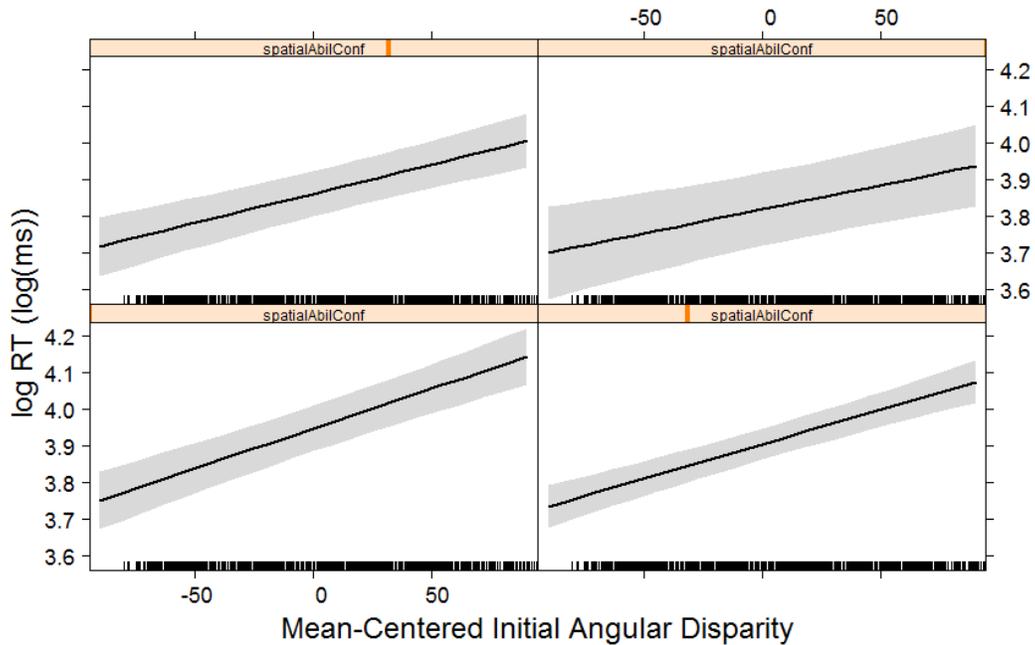


Figure 16. Experiment 2 effects display for the effect of the spatial ability / self-confidence factor and initial angular disparity on RT in the PRT_{NVF}. Bands depict 95-percent confidence interval.

Discussion

Experiment 2 had two goals. First we sought to replicate key findings from Experiment 1. Second, we addressed a limitation of Experiment 1, namely that participants received vivid visual feedback during the PRT (i.e. saw the figures move onscreen yoked to sensor manipulation). We designed the PRT

without visual feedback (PRT_{NVF}) to address this issue and used it to examine strategy use in the MRT.

Concerning the first goal, Experiment 2 replicated the main findings of Experiment 1. The PRT with visual feedback (PRT_{VF}), which was identical to Experiment 1's PRT, yielded statistically indistinguishable angular disparity effects (ADEs) compared to the mental rotation task (MRT), suggesting similarities between mental and physical rotation. Most importantly, the pattern of physical rotation data was nearly identical to Experiment 1. Participants physically rotated same figure pairs not to a match but rather to an off-axis orientation and different objects to a stable and distinct comparative. This successful direct replication has two implications. First, it further challenges the generally-held view that mental rotation involves rotation to a matching orientation. Second, it establishes a consistent pattern of behavior in the PRT task. When participants can freely manipulate SM figures in the MRT they reliably employ the strategy depicted in Figure 5.

We subsequently used this observation to inform our examination of physical rotation behavior in the PRT_{NVF} . In this task, participants rotated the handheld sensor to *mirror* their mental rotation but the onscreen figures remained static. However, we recorded the physical rotation data as if figure movement was yoked to the sensor. While this task did yield an ADE, the aggregated physical rotation data did not strongly resemble those from Experiment 1. Rather participants' behavior varied. In some cases, participants' data resembled Experiment 1, suggesting use of a motoric strategy because inferred mental

rotation processes resembled actual physical rotation. Yet, in other cases, data patterns suggested use of distinct cognitive strategies. We explored this further by applying data mining techniques to extract latent strategies from correct-response “same” trials (i.e. “hits”) in the PRT_{NVF} . We identified a motoric strategy, that resembled the physical rotation data from Experiment 1, and analytic strategies, in which participants limited movement of the sensor (i.e. “don’t move”) or moved it in a highly variable fashion.

It is an interesting observation that the PRT_{NVF} ’s motoric strategy, extracted by data-driven analyses, resembled the physical rotation data from Experiment 1’s PRT , given the differences between the two tasks. Even though the onscreen figures remained static in the PRT_{NVF} , participants often manipulated the sensor in a similar manner to Experiment 1, where they had vivid visual feedback. Recall that Experiment 2’s participants were instructed to manipulate the sensor to “mirror” their mental rotation process. Thus the pattern of physical rotation behavior in Experiment 1, and replicated in Experiment 2’s PRT_{VF} , appears to reflect a stable cognitive strategy used in the MRT. Because this behavior mimics actual physical rotation we suggest that it reflects use of mental rotation, a mental simulation strategy in which a mental percept is visuospatially transformed through intermediate orientations by means of covert motor rotation.

In contrast, the analytic “don’t move” strategy yielded a distinct physical rotation pattern. Here participants minimally moved the sensor, suggesting that they visually inspected the onscreen figures to make parity judgments rather than rotate their mental percepts. This finding is consistent with research showing that

individuals often use analytic strategies in spatial tasks which involve visually identifying key stimuli features and comparing stimuli using orientation-independent and rule-based strategies (Bethell-Fox & Shepard, 1988; Geiser et al., 2006; Glück & Fitting, 2003; Just & Carpenter, 1985; Schultz, 1991). Lack of sensor movement would be consistent with analytic strategies that involve such visual comparison.

Importantly, participants appeared to differentially bias mental rotation and analytic strategies based on task difficulty. Participants generally used the motoric strategy (i.e. mentally rotated) for easy (i.e. small angular disparity) trials and the “don’t move” strategy for difficult (i.e. large angular disparity) trials. Further this strategy profile was optimal regarding response time (RT). RT was faster for easy trials when participants mentally rotated. Likewise, RT was faster for difficult trials when participants used the “don’t move” strategy.

Individual differences analyses provided corroborating evidence for these conclusions. Concerning strategy use, self-reported spatial ability interacted with task difficulty. Relative to low, high-spatial participants were more likely to trade off between mental rotation and analytic strategies as difficulty increased. Further, this behavior appeared optimal with respect to RT, leading to marginally decreased ADEs. These results support the theory that a key component of spatial intelligence is the ability to trade off between mental simulation and analytic strategies (Hegarty, 2010). Contrary to our predictions, gender had an opposite effect on strategy bias, with males biasing mental rotation more than females. However, it is presently unclear if this difference is due to gender or differential

video game experience as these measures were anti-correlated. More research is needed to disentangle the contributions of these factors. Lastly, we neither observed main effects nor interactions of mental imagery vividness on strategy bias or RT. This suggests that vividness of the mentally rotated percept is not associated with differential strategy use in the MRT.

More broadly, these findings lend support to the multi-strategy view of mental rotation which states that mental rotation is covert motor simulation and that the classic MRT integrates both mental rotation and distinct analytic strategies. How strategies are used in the MRT is in turn influenced by a host of internal and external factors. Here we supported previous research that suggests that MRT strategy profiles are influenced by task difficulty (Glück & Fitting, 2003). Consistent with previous research we found that evidence suggesting mental rotation is biased for easy trials while analytic strategies are biased for difficult trials (Cochran & Wheatley, 1989; Ecker et al., 2008; Lohman & Kyllonen, 1983). This is an important findings considering that all MRT-based mental rotation research manipulates task difficulty in order to yield ADEs. Lack of consideration of the impact of task difficulty on MRT strategy use in the mental rotation literature may explain why the role of motor simulation in mental rotation remains a topic of debate (Zacks, 2008). Since task difficulty dynamically biases mental rotation and analytic strategies, we suggest that these strategies have been frequently conflated in discussions of mental rotation leading to misattribution of the behavioral outcomes and/or neural bases of one strategy for the other. Therefore it important for future research in this area to acknowledge

the impact of task difficulty on MRT strategies, taking care to separately consider mental rotation and distinct analytic strategies.

It is important to note that several limitations constrain the interpretation of these findings. While inferring cognitive strategies from physical rotation behavior is an exciting and novel methodology, it may have unintended and undesirable consequences. First, physically rotating the sensor may produce dual-task interference which could impact mental rotation performance (Van Selst & Jolicoeur, 1994). Our observation that high video game experience participants biased motoric strategies more than low lends some support to this claim. These individuals ostensibly have more experience translating intentions (e.g. move forward, fire weapon, etc.) into manual interactions. Second, sensor rotation itself may prime mental rotation, consistent with previous research (Flusberg & Boroditsky, 2011; Kosslyn et al., 2001; Wiedenbauer et al., 2007). For example, longer motoric strategy RTs for difficult trials may stem from self-generated interference from physical rotation. Third, Experiment 2's instructions may have biased mental rotation. Participants were instructed to "mirror" their mental rotation by manipulating the sensor. These instructions may have suggested that mental rotation was the preferred strategy in the task. Fourth, our strategy extraction methodology quantitatively assigned individual trials to one of three strategy clusters: mental rotation, "don't move," and high variability. While quantitative strategy classification is less susceptible to experimenter bias it may have wrongly categorized clusters. For example, the low angular disparity motoric trials best resembled the data from Experiment 1 but also involved minimal

rotation, characteristic of the “stay same” strategy. Lastly, cognitive strategies gleaned from physical rotation likely conflate mental rotation sub-strategies (effector- vs. object-based rotation). While we have suggested that both sub-strategies can be considered covert motor rotation, researchers interested in distinguishing between these sub-strategies may find measures of physical rotation behavior inadequate.

Despite these limitations, Experiment 2 leads to two conclusions. First, the PRT_{VF} data shows that when participants physically rotate figures in the MRT they use a stable strategy involving rotation to an off-axis orientation. Second, the PRT_{NVF} data suggest that individuals flexibly integrate mental rotation and analytic strategies in the MRT based on task difficulty.

Interim Conclusions

Together Experiments 1 and 2 support the multi-strategy view of mental rotation. We replicated the similarities between mental and physical rotation as well as the physical rotation patterns observed in Experiment 1, supporting the first claim that mental rotation is covert motor simulation. Further data mining the PRT_{NVF} data supported the second claim that strategy use in the MRT is influenced by task difficulty, an important consideration given the ubiquity of difficulty manipulation in the mental rotation literature. Broadly this finding supports the claim that the MRT and other spatial tasks integrate more than one cognitive strategy, including mental rotation and analytic strategies. Dynamic strategy use may be a domain-general cognitive principle and gaining better

understanding of strategies used in spatial tasks may yield novel insights in other cognitive domains (Taylor & Brunyé, 2013).

Motivations for Experiment 3

Together, Experiments 1 and 2 support the multi-strategy view using novel behavioral tasks. These tasks infer cognitive strategies from physical rotation behavior. Inferences from Experiment 2's PRT_{NVF} suggest flexible integration of mental rotation and analytic strategies, consistent with previous work. Yet, it is not clear whether the act of physical rotation influences the underlying mental rotation process. It is possible that the window into mental rotation that physical rotation provides also contaminates the cognitive process, a cognitive observer effect. This relates to a broader limitation of behavioral research in general. Implicit behavioral measures, such as accuracy and response time, are not well-suited for inferring strategy use in spatial tasks. In contrast, explicit measures, such as self-report or think-aloud protocols, have provided novel insights (Glück & Fitting, 2003; Lohman & Kyllonen, 1983; Schultz, 1991; Taylor & Tenbrink, 2013) but these measures have been shown to prime strategy use (Glück, Duenser, Steinbuegl, & Kaufmann, 2007).

One way to address this limitation is to use neuroscientific techniques to infer cognitive processes. Neuroscience-based methods can classify cognitive strategies in real time while avoiding unintended strategy bias. As reviewed above, neuroimaging research has shown that mental rotation is associated with neural activation in motor cortical areas. Observing motor cortex activation in the

MRT may be a fruitful way to passively investigate strategy use in spatial tasks while avoiding introduction of bias.

EXPERIMENT 3

Introduction

The neuroscientific literature has been equivocal concerning the role of motor simulation in mental rotation. Several experiments have observed motor cortical activation in the MRT but many others have not (Zacks, 2008). Variable motor activation likely reflects *flexible* use of mental rotation, consistent with the multi-strategy view. Flexible strategy use in the MRT makes observing motor activation a moving target and limitations of common neuroimaging techniques complicate their use for MRT strategy classification. While high spatial resolution techniques, such as fMRI, have been instrumental in identifying specific motor areas implicated in mental rotation, these methods are expensive and importantly lack temporal resolution. This makes it difficult to classify strategy use from trial to trial or even within single trials. Yet, as Experiment 2 and previous research suggests, strategy use in the MRT is dynamic and influenced on a trial by trial basis by task difficulty. Therefore, moving forward, it is important to apply temporally sensitive neuroscientific measures of motor activation to MRT research.

One technique that appears to be well-suited for neuroscientific inquiry into MRT strategy profiles is scalp electroencephalography (EEG). EEG has high temporal resolution on the order of milliseconds and is relatively inexpensive to collect. Thus EEG may be able to classify dynamic strategy use in the MRT.

Research using the event-related potential (ERP) technique has commonly demonstrated an association between mental rotation and a parietal-centered late positive component between ~350 – 800 ms (Bajric, Rosler, Heil, & Hennighausen, 1999; Heil & Rolke, 2002; Milivojevic, Hamm, & Corballis, 2011; Milivojevic, Johnson, Hamm, & Corballis, 2003; Peronnet & Farah, 1989; Riecanisky & Jagla, 2008; ter Horst, Jongsma, Janssen, Lier, & Steenbergen, 2012). Further the negativity of this component increases concomitant with angular disparity. This “rotation-related negativity” (RRN) has been interpreted as a neurophysiological correlate of mental rotation (Heil, 2002). In addition, it is important to note that if a spatial task is solved without mental rotation (i.e. with analytic strategies) then RRN is conspicuously absent from the ERP (Bajric et al., 1999; Heil, Rauch, & Hennighausen, 1998). Thus ERP-based mental rotation research supports the multi-strategy view’s claim that the MRT integrates both mental rotation and distinct analytic strategies. However, ERP-based research is ill-equipped to address the first claim of the multi-strategy view, that mental rotation is covert motor simulation. This is because EEG lacks the spatial resolution necessary to record activation in motor areas. However, analysis of EEG spectral power can indirectly measure motor cortical activation and may be able to classify use of mental rotation in the MRT.

Mu suppression is an EEG correlate of motor simulation that holds great promise for online classification of cognitive strategies in the MRT. The sensorimotor mu rhythm (AKA mu wave) is an EEG oscillation generated in the sensorimotor cortex (Pineda, 2005). Its dominant frequencies lie in the 8 - 13 Hz

band, overlapping the classical alpha band (Bazanov & Vernon, 2014), with a strong first harmonic in the beta band centered around 20Hz. The two harmonic peaks of the mu rhythm give its power spectral density function its characteristic shape which resembles the Greek letter mu. Under an idling state, mu rhythms are synchronized (Pfurtscheller, Stancak, & Neuper, 1996). However, motor simulation results in event-related desynchronization (ERD) of the mu rhythm, marked by reduction of power in the mu-specific frequency band as measured by the squared amplitude of the oscillation. Research has demonstrated that self-initiating goal-directed movement, such as reaching or grasping, as well as preparing to move or observing others' movements desynchronizes (or suppresses) mu rhythms (Llanos, Rodriguez, Rodriguez-Sabate, Morales, & Sabate, 2013; Muthukumaraswamy, Johnson, & McNair, 2004; Pfurtscheller & Lopes da Silva, 1999). Notably, even *imagining* movement execution can elicit mu suppression (Francuz & Zapala, 2011; McFarland, Miner, Vaughan, & Wolpaw, 2000; Pfurtscheller & Neuper, 1997), an important consideration given that mental rotation presumably involves motor imagery.

Mu suppression has also been linked with activation in cortical motor areas. It is generally accepted that alpha band desynchronization reliably reflects excited cortical networks (Feige et al., 2005; Goldman, Stern, Engel, & Cohen, 2002; Goncalves et al., 2006; Laufs et al., 2003; Laufs et al., 2006; Pfurtscheller et al., 1996). In line with this assertion, mu suppression is thought to reflect modulation of motor neurons in the premotor cortex (Pineda, 2005) and recent research has shown that mu suppression is associated with BOLD response in

premotor and sensorimotor cortices (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Formaggio, Storti, Cerini, Fiaschi, & Manganotti, 2010; Mizuhara, 2012; Perry & Bentin, 2009; Ritter, Moosmann, & Villringer, 2009; Yuan et al., 2010; Zich, Debener, et al., 2015). Therefore when mu suppression is observed it can be reasonably assumed that motor cortical areas are also active. This feature of mu suppression makes it a promising methodology to apply to investigations of mental rotation, particularly for cognitive processes that depend, in part, on neural computations that subserve motor planning. Indeed, mu suppression appears to combine the temporal resolution of EEG, which is useful for inferring real-time strategy use in the MRT, with the ability to discern motor cortical activation, which is useful for classifying strategy use.

Recent work has begun to apply this methodology to examine cognitive strategies in spatial tasks. Chen, Bin, Daly, and Gao (2013) recorded EEG while participants completed a hand laterality judgment task (HLT); participants judged whether rotated hand images were right or left hands. This task is well-suited for investigating mental rotation (particularly effector-based) because it uses corporeal stimuli and is thought to depend on motor imagery (Parsons, 1994). In each trial, participants first viewed a fixation cross followed by a rotated hand stimulus that remained onscreen until the participant responded. The researchers observed reductions in mu-band power (i.e. mu suppression) over central and parietal regions during the stimulus epoch relative to the fixation epoch. Further, mu suppression magnitude and RT were negatively correlated, suggesting that reductions in mu-band power reflect mental rotation.

Complementary evidence demonstrates that mu suppression can discriminate between different strategies in the HLT. Classic HLT studies demonstrated that RT for hand stimuli increases with greater rotation from an upright posture, but this function is not linear, unlike with SM figures. Rather, physically awkward or impossible to perform hand postures increase RT substantially, suggesting that mental rotation of hands involves mentally simulating the rotation of one's own hand (Cooper & Shepard, 1975; Decety, 1996; Jeannerod, 1994; Parsons, 1987a; Parsons, 1987b; Sekiyama, 1982). Concerning strategy use, individuals should be less likely to mentally rotate in the HLT when depicted hand postures are biomechanically difficult or impossible to adopt and thus difficult to mentally simulate. Instead, they may favor analytic strategies that do not involve mental simulation of one's own hand. Recently, ter Horst, Lier, & Steenbergen (2013) recorded EEG while participants completed a HLT. They found that biomechanically easy-to-perform hand postures elicited greater mu suppression than biomechanically difficult- or impossible-to-perform postures. This finding suggests that mu suppression can distinguish between mental rotation and analytic strategies in the HLT.

The findings reviewed above suggest mu suppression observed in the HLT reflects the use of motor simulation (i.e. mental rotation). However, an alternative explanation is that mu suppression simply reflects cognitive load induced by task difficulty (Klimesch, 1999). Recent findings lend support to the former account. Osuagwu and Vuckovic (2014) recorded EEG while participants completed an explicit motor imagery task (imagined hand closing) and the HLT. As expected,

they observed mu suppression in both the motor imagery task and the HLT. Importantly, within-participants time-frequency analysis and source localization of the EEG revealed highly similar spatial and time-frequency characteristics for the two tasks. This finding supports the claim that mental rotation used in the HLT relies on motor simulation. Taken together, EEG investigations of the HLT suggest that measuring mu suppression may be a fruitful methodology for inferring when mental rotation is used in the MRT.

Some research has investigated alpha (α) band power in the MRT. Gill, Boyle, and Hathaway (1998) examined EEG correlates of theorized subcomponent processes of mental rotation: a) stimuli encoding, b) image generation, c) mental rotation and comparison, and d) match/no-match decisions (Just & Carpenter, 1976). Their findings suggest that the left temporal and left parietal areas were most engaged (i.e. yielded maximal α -band suppression) during image generation and mental rotation, respectively. However, this study has limited implications for the multi-strategy view due to aspects of its design. Mu suppression is typically investigated from central electrode sites (C3, Cz, C4) located over sensorimotor cortex. However, the researchers used an 8-electrode array that did not include these sites. Further, they did not investigate the effect of task difficulty on α band power, a factor that may influence strategy use in the MRT. Lastly, their investigation only included male participants, precluding an examination of gender effects. Similarly, Williams et al. (1995) found reductions in parietal α power in the MRT as well as task-related reductions in frontal α power, which they interpreted as evidence for motor simulation. However, they

too neither considered central electrode sites nor task difficulty effects and had unequal gender representation in their sample.

Other studies have found higher levels of mu suppression duration and magnitude associated with increased RT in Cooper and Shepard's (1973) alphanumeric MRT (Michel, Kaufman, & Williamson, 1994; Riečanský & Katina, 2010). However, these studies likewise averaged spatially broad electrode sets over central, parietal, and occipital areas confounding electrophysiological contributions of different cortical areas. Further, two- and three-dimensional MRTs may possess different strategy profiles, with the former biasing mental rotation and the latter eliciting both mental rotation and analytic strategies (Bauer & Jolicoeur, 1996). Thus findings for one MRT may not generalize to the other.

In order to lend empirical support to the multi-strategy view and the central findings of Experiment 2 it is important to demonstrate that performance in the classic MRT activates motor cortical areas and that strategy use varies due to task difficulty. But to date no EEG-based research has applied mu suppression to make these empirical observations. Experiment 3 takes a first step in this direction. Participants completed a standard MRT of SM figures while EEG data were collected. We conducted spectral power analyses on these data using two different and complementary techniques. Our predictions were informed by the details and capabilities of these techniques. As such, we will describe them before stating our predictions.

First we used existing best-practice electrode-based methodologies to compare and connect our findings with the existing literature. Research suggests

that broad-band mu (8 - 13 Hz) may actually be comprised of two distinct higher and lower frequency bands whose reactivity patterns differ in motor tasks (Pineda, 2005; Pfurtscheller, Neuper, & Krausz, 2000). Lower mu (8 – 10 Hz) is spatially widespread over central and parietal areas and is thought to reflect a distributed neural network that is activated by different types of motor behavior, but is not critical to support a specific movement. In contrast, upper mu (11 – 13 Hz) is more spatially focalized and somatotopically specific. Further, relative to lower mu, changes in upper mu power are less sensitive to general cognitive demands, such as attention processes (Klimesch, 1999). For these reasons we focused our investigations on the upper mu band.

We also considered individual variability of the frequency range of the mu rhythm. When examining α -band power, researchers commonly define an individual α frequency (IAF) for each participant by determining the α -band frequency that is maximally suppressed during the cognitive task of interest (Bazanov & Vernon, 2014; Klimesch, 1999). However, one criticism of this technique is that it is circular. Analysis of task performance that only considers frequencies that yield maximal suppression may bias the analysis towards significance. To address this criticism we defined a *motor-imagery based IAF* for each participant. In addition to the MRT, participants completed a commonly-used motor imagery task and we computed an upper mu IAF from this task and used it in the MRT analyses.

In addition to the electrode analyses we also applied cutting-edge analysis techniques that decompose recorded EEG data using independent component

analysis (ICA; Makeig, Debener, Onton, & Delorme, 2004; Onton, Westerfield, Townsend, & Makeig, 2006). EEG data collected at electrode sites do not reflect electrical activity generated solely from underlying proximal cortex. Rather, EEG sources project near-instantly to and sum linearly at all scalp electrode sites via volume conduction (Davidson, Jackson, & Larson, 2000). ICA is a mathematical blind source separation technique that decomposes the mixed EEG signals collected from electrodes into a set of temporally, functionally, and spatially independent signals (or information sources) (Bell and Sejnowski, 1995; Jung et al., 2001; Makeig, Bell, Jung, & Sejnowski, 1996). These ICA-derived components (ICs) reflect spatially-distinct, partially-synchronous local cortical field activities that can in turn plausibly reflect specific cognitive processes, such as motor imagery, visual perception, and working memory, as well as stereotypical artifacts, such as eye movements and blinks (Delorme, Palmer, Onton, Oostenveld, & Makeig, 2012; Makeig & Onton, 2012; Onton, Delorme, & Makeig, 2005). Thus, ICA can both attenuate the effects of source mixing by volume conduction as well as extract brain- and non-brain- related signals embedded in raw EEG recordings.

This methodology has several advantages for investigating cognitive strategies in the MRT. First, both motor- and parietal-localized cognitive processes contribute to mental rotation (Zacks, 2008). Alpha band activity from these distinct processes is certainly mixed at central electrode sites via volume conduction, making it difficult to separate their independent contributions. Indeed, motor and parietal α -band activities may actually *oppose* each other. Previous

research has demonstrated that as task difficulty in the MRT increases, parietal α -band power *decreases* (Michel et al., 1994; Riečanský & Katina, 2010; Williams et al., 1995). Yet, Experiment 2's findings suggested that mental rotation decreases with increasing difficulty. Consistent with this finding, increasing task difficulty should be associated with motor α -band power *increases*. Thus, opposing task difficulty-dependent changes in motor and parietal α -band power may cancel each other out when recorded simultaneously at central electrode sites. Notably, several studies using ICA decomposition have identified independent motor and parietal/occipital α ICs (Behmer & Fournier, 2014; Gramann et al., 2010; Grandchamp, Braboszcz, Makeig, & Delorme, 2010; Huang, Jung, Delorme, & Makeig, 2008; Makeig et al., 2002; Manshanden, De Munck, Simon, & Lopes da Silva, 2002; Naeem, Brunner, Leeb, Gramann, & Pfurtscheller, 2006; Wang & Makeig, 2009). Thus measuring α -band power separately for motor and parietal ICs in the present experiment may yield novel insights into the interplay of their contributions to cognitive processing in the MRT.

Second, other well-documented ICs may reflect use of analytic strategies in the MRT. Several studies have observed a frontal midline theta (fm θ) (5 – 7 Hz) IC. Generated in the anterior cingulate cortex (ACC) and surrounding dorsomedial prefrontal cortex (DMPFC) (e.g., Ishii et al., 2014; Oehrns et al., 2014), fm θ power is associated with several higher-order cognitive processes, including active working memory maintenance / manipulation, cognitive control, and sustained attention (Cavanagh & Frank, 2014; Gevins & Smith, 2000; Gevins, Smith, McEvoy, & Yu, 1997; Hanslmayr et al., 2008; Hsieh & Ranganath, 2014;

Itthipuripat, Wessel, & Aron, 2013; Jensen & Tesche, 2002; Klimesch, 1999; Maurer et al., 2015; Onton et al., 2005; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007; Scheeringa et al., 2009). For example, Onton and colleagues (2005) found that power increases in the fm θ IC were associated with increases in visual working memory load. Analytic strategies in the MRT involve visual identification and comparison of key stimuli features using orientation-independent and rule-based strategies. These strategies are likely working memory intensive and thus use of these strategies may be reflected in fm θ power.

Having established the present methodology, we now detail our predictions. Recall that the multi-strategy view of mental rotation makes two claims. The first claim is that mental rotation is covert motor simulation. Given that mu suppression is an electrophysiological marker of motor simulation/imagery and mental rotation is frequently used in the MRT, we predicted that mu suppression would occur, both at central electrode sites as well as for motor ICs. This finding would support the claim that mental rotation depends on motor simulation. We also expected reductions in parietal α power, consistent with previous research (Gill et al., 1998; Michel et al., 1994; Riečanský & Katina, 2010; Williams et al., 1995).

The second claim is that participants not only use mental rotation in the MRT but also analytic strategies, differentially biasing the two based on internal and external factors. While mental rotation involves covert motor simulation, analytic strategies are thought to rely on working memory intensive visual comparisons. As such we predicted fm θ IC power enhancement would occur in

the MRT. Concerning dynamic strategy use, Experiment 2's finding that participants differentially biased strategies based on task difficulty informed our predictions. We expected to find converging evidence suggesting increased mental rotation for easy trials and increased analytic strategy use for difficult trials. Specifically for the electrode data we expected that central electrode mu suppression would be prominent for easy trials but reduce as difficulty increased. For IC analyses, we expected to find the same difficulty-dependent decrease in mu suppression for the motor ICs. Extending this finding, we also predicted a difficulty-dependent *increase* in fm θ IC power. Together observation of motor IC mu suppression for easy trials and fm θ IC power enhancement for difficult trials would provide strong evidence that participants dynamically bias mental rotation and analytic strategies in the MRT based on task difficulty.

In addition, we predicted that these effects would vary due to individual differences. In Experiment 2, we found that spatial ability interacted with MRT strategy use. Relative to low, high-spatial participants were more likely to trade off between mental rotation and analytic strategies. We predicted a similar result in the present data. Specifically, relative to low, high-spatial participants would more prominently yield the predicted difficulty-dependent decrease in mu suppression and increase in fm θ power. This would reflect the better ability of high-spatial participants to trade off between mental rotation and analytic strategies as difficulty increases. We also predicted gender effects in the present experiment. Male and female behavioral performance and neural activation patterns are largely similar for MRTs using corporeal stimuli but diverge with SM

figures (Alexander & Evardone, 2008; Jordan et al., 2002; Seurinck et al., 2004). This finding suggests that males utilize analytic strategies more than females in the classic MRT. In addition, females elicit more mu suppression than males when watching hand actions (Cheng et al., 2008). In line with these findings, we predicted that females would elicit more mu suppression than males. Further, if males bias analytic strategies more than females, they should more prominently yield the predicted difficulty-dependent increase in fm θ IC power.

Method

Participants

Thirty-two right-handed Tufts University students (mean age = 19.2 years; 16 male, 16 female) participated for monetary compensation.

Materials

Figures and Stimuli Presentation. We used SM figure images taken from Peters and Battista's (2008) stimulus library. We selected eight of the 15 figures used in Experiment 1. Selected stimuli fully crossed the items analysis factors (e.g. arm weighting and symmetry) discussed in Experiment 1. We then combined stimuli into 224 pairs, fully crossing eight stimuli, two trial types (same, different), and seven angular disparities ($0^\circ, \pm 30^\circ, \pm 60^\circ, \pm 90^\circ, \pm 120^\circ, \pm 150^\circ, 180^\circ$). Each stimuli pair image was 1480 x 720 pixels in size and stimuli were horizontally separated by a centered 40 x 40 pixel cross. Stimuli and EEG event markers were presented using PsychoPy (Peirce, 2007), software version 1.81.03 on a 1920 x 1200 resolution LCD monitor. We used a photo sensor (see Auxiliary Peripherals

section below) for time locking to stimuli onset. Participants recorded their responses with USB hand-held button switches (Delcom Products).

Questionnaires. We retained the questionnaire set from Experiment 2, including an additional self-report questionnaire of motor imagery vividness, the VMIQ-2 (Roberts, Callow, Hardy, Markland, & Bringer, 2008). Table 7 presents the summary statistics of questionnaire responses for Experiment 3's sample.

Table 7. Experiment 3 individual difference measures.

Individual Difference	Questionnaire/Assessment	Statistics & Interpretation
Spatial ability	Santa Barbara Sense of Direction Scale (Hegarty, et al., 2002)	Moderate sense of direction $M = 4.5$, scale: 1 - 7
Spatial self-confidence, survey strategy, and knowledge of cardinal directions	English FRS questionnaire on spatial strategies (Münzer & Hölscher, 2011)	Moderate self-confidence in spatial abilities $M = 4.5$, scale: 1 - 7 Moderate preference for survey strategies $M = 3.9$, scale: 1 - 7 Low knowledge of cardinal directions $M = 2.6$, scale: 1 - 7
Video game experience	Video game experience questionnaire (Boot et al., 2008)	Moderate-low video game frequency $M = 1.2$ hours per week
Handedness	Edinburgh Handedness Inventory (Oldfield, 1971)	Large right hand bias $M = 1.5$ scale -2 (LH) - +2 (RH) all participants self-reported right handed
Vividness of Mental Imagery	VVIQ-2 (Marks, 1995)	Moderate-high mental imagery vividness $M = 3.5$, scale 1 - 5
	--- Shapes Questionnaire (Dean & Morris, 2003)	--- Moderate-high ease of mental imagery formation $M = 6.6$, scale 1 - 9 Moderate pictorial instability of mental imagery $M = 4.5$, scale 1 - 9 Moderate ease of mental imagery rotation $M = 5.6$, scale 1 - 9 Moderate relative size of mental imagery $M = 5.1$, scale 1 - 9

Table 7 (continued).

Individual Difference	Questionnaire/Assessment	Statistics & Interpretation
Vividness of Motor Imagery	VMIQ-2 Roberts et al., 2008	High kinesthetic motor imagery vividness $M = 4.1$, scale 1 – 5 High internal motor imagery vividness $M = 4.1$, scale 1 – 5 Moderate-high external motor imagery $M = 3.6$, scale 1 – 5

EEG Recording. We used a 32-channel electrode configuration in an active electrode cap (ActiCap, Brain Products) according to the international 10-20 system (see Figure 17 for electrode locations). A ground electrode was placed over Fpz. Scalp impedances of electrodes were kept below 35 k Ω by use of conductive gel and mild scalp abrasion. EEG data were collected reference-free on a computer running BrainVision PyCorder and amplified by a BrainVision ActiChamp active channel amplifier, sampled at a 1 kHz sampling rate, with a 60 Hz notch filter applied online. EEG data were subsequently bandpass filtered offline between 1 and 40 Hz and referenced to averaged mastoids (TP9 & TP10).

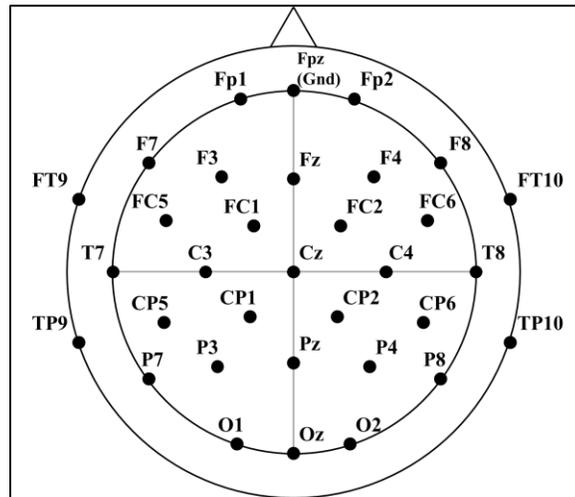


Figure 17. Experiment 3 32-channel electrode montage.

Auxiliary Peripherals. We connected a Brain Products Photo Sensor to the ActiChamp. This small sensor was located at the top right corner of the stimulus presentation screen and was used to insert event markers in the EEG to record precise stimuli presentation timing. We also connected a Brain Products 3-D Acceleration Sensor which was affixed to the participant's right hand during the experiment to record accidental movement for the purpose of trial rejection.

Procedure

Participants sat in an armchair approximately one meter from the computer screen. Participants first completed the questionnaires and then the experimenter affixed the EEG cap, prepared the electrodes, and affixed the acceleration sensor to the right hand. Then the experimenter detailed the experiment instructions. The experimenter instructed participants to decide on each trial whether the two onscreen SM figures were same or different, taking care to not use the term rotation in order to avoid inadvertently biasing mental rotation. The experimenter then familiarized participants with the trial structure (see Figure 18).

Each trial began with a fixation cross that was presented for 2000 ms. Then a rotated SM figure pair was presented for 5000 ms. A 3000 ms response screen followed during which participants recorded their parity judgement by pressing one of two handheld buttons. The “same” response was always mapped to the right button and “different” was always mapped to the left. Lastly, a 1000 ms blank screen appeared in preparation for the next trial. The experimenter emphasized that participants should respond only during the response screen and to otherwise keep their hands still holding the buttons in their lap. This served to prevent mu suppression by motor preparation or execution of the button response from contaminating the stimuli epoch. Participants completed 224 randomized order trials, taking a one minute break after every 60 trials. Participants were permitted to extend breaks indefinitely if they wished.

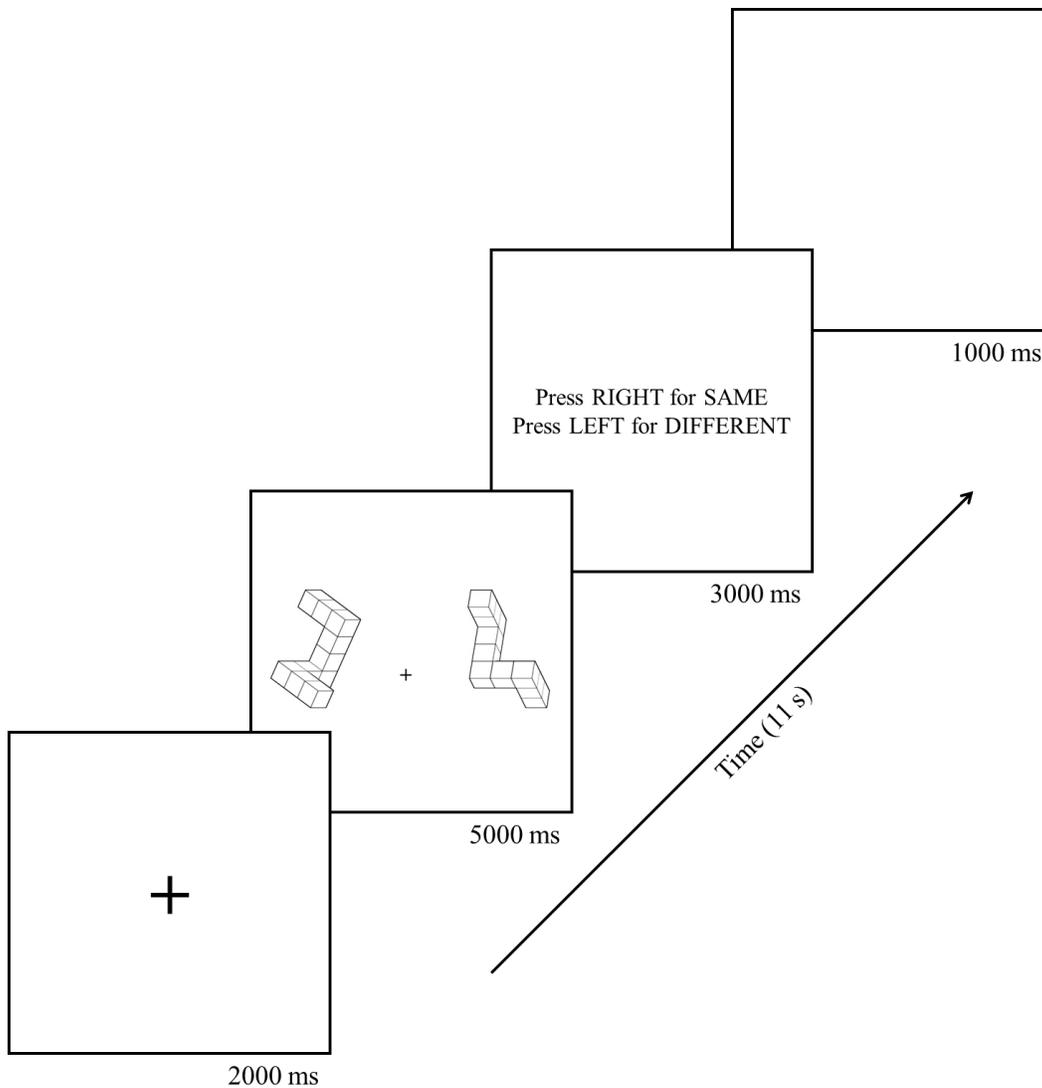


Figure 18. Experiment 3 main experiment trial structure.

Following the main experiment participants completed a motor imagery (MI) task. In this task (see Figure 19 for trial structure), participants viewed either a left or right arrow on screen and imagined clenching their corresponding fist. This task served two purposes. First, as similar MI tasks reliably induce mu suppression (Francuz & Zapala, 2011; Llanos et al., 2013; Pfurtscheller, Brunner, Schlögl, & Lopes da Silva, 2006; Pfurtscheller & Neuper, 1997), this task served as check on our EEG apparatus and spectral power analyses. Second, we

determined the dominant frequency in the upper mu range that maximally suppressed in this task for each participant. We subsequently used this information to inform analyses of the MRT data. Participants completed 30 randomized trials (15 left, 15 right). Upon completion of this task participants were debriefed and compensated.

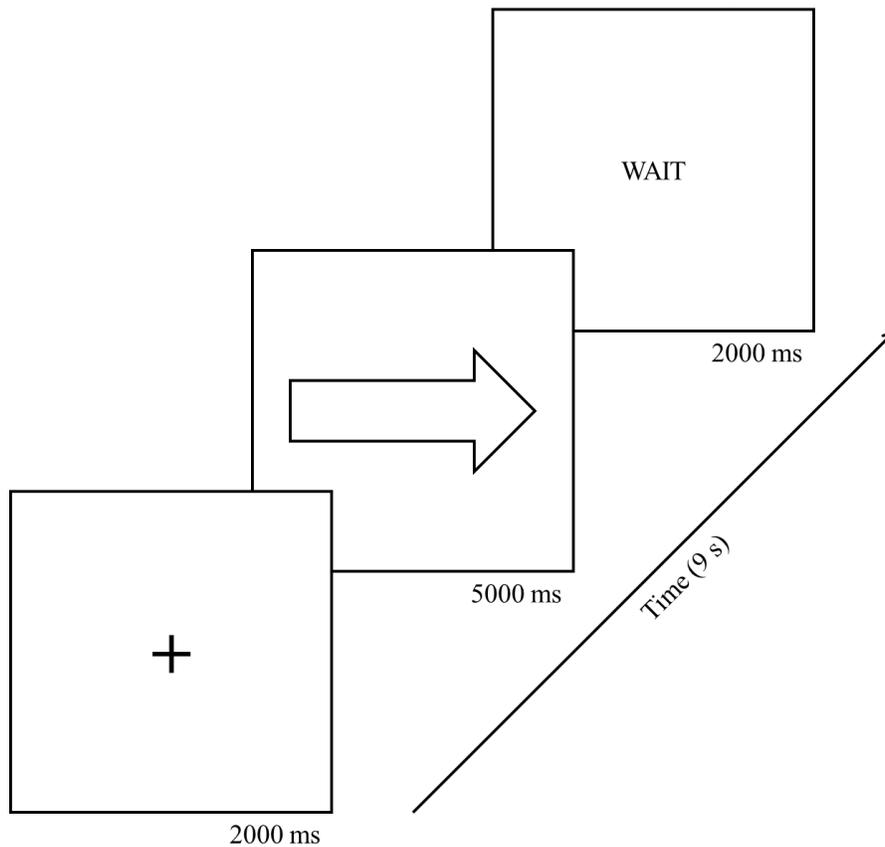


Figure 19. Experiment 3 motor imagery task trial structure.

Data Preprocessing and Analyses

Preprocessing and Trial Rejection

We conducted all EEG preprocessing and analysis using EEGLAB (Delorme & Makeig, 2004), software version 13.4.4b, implemented in MATLAB

(The Mathworks, Inc.). Our preprocessing stream involved *semi-automated* epoch rejection coupled with visual inspection of ICA-decomposed EEG data. This approach more reliably detects artifacts than using raw scalp data (Delorme, Sejnowski, & Makeig, 2007). Further, ICA decomposition is an excellent technique for artifact *correction*. Recall that ICA decomposes the mixed EEG signal into a set of independent components (ICs) that reflect brain-related signals as well as stereotypical artifacts. Commonly observed artefactual ICs, such as eye blinks and eye movements, are readily apparent upon visual inspection of IC scalp maps. These artefactual ICs can be subtracted from the data and the remaining ICs can then be reconstructed back into the mixed signal, yielding EEG data in which non-neural artifacts are greatly attenuated. Artifact correction using ICA in this manner is generally considered superior to regression-based artifact correction techniques (Hoffmann & Falkenstein, 2008). In the following section we detail the preprocessing, epoching, and analysis procedures that we applied to each participant's raw EEG data for both the MRT and MI tasks.

Initial Processing and Epoching. Prior to epoching the data, we first extracted temporally precise event markers from the photo sensor data using a custom script that marked the onset of the fixation cross and the SM figure stimuli. Then, after bandpass filtering and referencing the data, we removed flat channels possessing kurtosis > 5 automatically and poorly connected (i.e. popping) channels by visual inspection. Next, we selected a subset of electrodes to improve the signal to noise ratio in our dataset. Excessive noise, such as caused by poorly-connected electrodes or complex movement artifacts, reduces ICA

decomposition quality. Poor quality decompositions yield several single-channel and/or noisy ICs which in turn reduce the number of remaining components that reflect brain signal. To prevent this we selected a subset of 19 electrodes to submit to ICA decomposition. This subset included all frontal, fronto-central, central, and parietal electrodes located within the “inner circle” of the montage (see Figure 17) as well as the frontal electrodes above the eyebrows (Fp1 & Fp2) in order to capture ocular artifacts for subsequent removal. We chose to exclude temporal and occipital sites because these electrodes often possessed poor scalp adhesion and were prone to noise. Then, for the MRT, we defined 6.8 second epochs initiating 200 ms after the visual onset of the fixation cross and extending until the end of the five second stimuli presentation. These epochs contained only baseline and mental rotation-related EEG data and excluded visual evoked potentials at baseline onset and data collected during the manual button response. For the MI task we defined 3.8 second epochs likewise initiating 200 ms after the visual onset of the fixation cross and extending until two seconds after stimuli onset. Epochs containing similar amounts of MI-related data (1 – 2 s) have successfully observed mu suppression (Francuz & Zapala, 2011; Llanos et al., 2013; Pfurtscheller et al., 2006; Pfurtscheller & Neuper, 1997).

Epoch Rejection. We first rejected epochs in which participants excessively moved using the acceleration sensor data. Prior to data collection, we ran a pilot experiment in which a participant performed gross motor movements of varying magnitude during the stimuli presentation window. Using this data, we computed the mean standard deviation (mSD) of the three axes (x,y,z) of the

acceleration sensor data during each movement trial and then computed the minimum mean. Using this value as a threshold, we rejected MRT epochs that possessed $mSD > \text{threshold}$. We then identified epochs with paroxysmal data by automatically rejecting epochs containing EEG values in excess of $\pm 500 \mu V$. We stepped down this threshold in $50 \mu V$ increments until $\pm 100 \mu V$, visually inspecting rejected epochs at each step. When the threshold was low enough to reject eye blinks we ceased rejection, retaining these artifacts in the data. We then downsampled the data to 250Hz and conducted extended infomax ICA, using EEGLAB's runica algorithm.

Next, we plotted and visually inspected IC scalp maps to identify artefactual components. Components depicting bilaterally symmetric voltages over anterior sites were noted as blink-related artifacts. Components depicting bilaterally asymmetric opposite polarity voltages over anterior sites were noted as eye movement-related artifacts. Figure 20 depicts examples of these commonly observed ocular artefactual components.

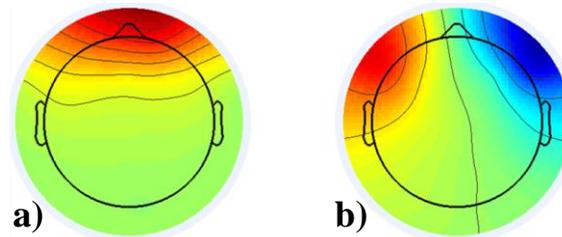


Figure 20. Examples of ICA components of commonly occurring ocular artifacts: eye blink-related artifact (a), horizontal eye movement-related artifact (b).

We then conducted semi-automatic epoch rejection on the remaining ICs using EEGLAB's native functions. We marked epochs with abnormal spectra ($+25 \text{ dB} < \text{power} < -100 \text{ dB}$, 20 – 40 Hz) and abnormal values ($+25 < \text{std dev} < -25$) to capture muscle artifacts, using the pop_eegthresh and pop_rejspec

functions, respectively. For some participants we increased these thresholds to ± 30 dB to avoid mis-rejecting ongoing α activity. We then visually inspected and confirmed the automatic rejections, reversing erroneous rejections of α activity. Following rejection of epochs containing artifacts we conducted a second ICA decomposition on the pruned dataset and saved the resulting weights. Lastly, we returned to the original dataset (1000 Hz sampling rate), rejected the marked epochs identified previously, and loaded the saved ICA weights.

At this stage, we localized a best-fitting single equivalent dipole corresponding to each IC using a single equivalent dipole in a best-fitting spherical four-shell head model (BESA) using the DIPFIT2 toolbox in EEGLAB (Oostenveld & Oostendorp, 2002; available from scn.ucsd.edu/eeglab/dipfit.html). This procedure involved warping the standard 10-20 electrode coordinates of the electrode subset to the BESA head model followed by automated coarse and fine-fitting to the spherical wire matrix. Dipole fitting attempts to spatially locate the cortical source patch of a given IC scalp map by hypothesizing a dipole source that could have generated the scalp map's potential distribution and then computing the forward model that explains the highest percentage of the variance in the scalp map. Spatial localization of IC sources is helpful for identifying comparable ICs across participants, such as motor or $\text{fm}\theta$ components.

Lastly, we subtracted the eye-related ICs visually identified previously, yielding raw EEG data in which blink and eye movement artifacts were greatly attenuated. These artifact-rejected and ICA-corrected data were used in

subsequent analyses. In total, our preprocessing and epoch rejection procedure removed 7.3% of MRT trials and 4% of MI task trials.

Data Analyses

Independent Component Clustering. Prior to computing spectral power we sought to identify similar ICs in the MRT data across participants. We were specifically interested in motor ICs that show characteristic mu suppression as well as fm θ ICs that may reflect working memory load. To accomplish this we used component clustering techniques implemented in EEGLAB. Prior to clustering we removed ICs that were previously visually identified as artefactual (see Figure 20) as well as ICs that had more than 15% residual variance from the spherical forward-model scalp projection. However, inconsistent with common practice (see: Onton et al., 2005), we retained ICs with dipoles located outside the brain volume. We observed several sensorimotor-localized ICs with dipoles just outside of the head but further inspection of their power spectra suggested these ICs were non-artefactual. It is possible that the relatively small set of electrodes ($n = 19$) used in our data analysis reduced the spatial localization accuracy of dipole fitting. Nevertheless we decided to retain these ICs to improve our analyses' statistical power. This procedure reduced the number of ICs in the dataset from 603 to 465. The mean number of ICs retained for subsequent clustering was ~15 per participant.

Both motor and fm θ ICs are characterized by their power spectra and the spatial locations of their neural generators. As reviewed above, the mu rhythm has spectral power peaks centered around 10 and 20 Hz and is localized within the

sensorimotor cortex while fm θ ICs have peak power in the 5 – 7 Hz range and are localized in the ACC and DMPFC. As such we precomputed IC power spectra with fast Fourier transform (FFT) and used these values along with the precomputed dipole coordinates to cluster ICs. EEGLAB uses principle component clustering methods to reduce data dimensions prior to clustering. We reduced spectral data to 10 dimensions but kept dipole locations to their original 3 dimensions. We equally weighted spectra dimensions and dipole locations, combined them into a single matrix, and applied k-means cluster analysis to the matrix, extracting 15 IC clusters. ICs whose distance to any cluster centroid was larger than three standard deviations from the mean were separated into an outlier cluster. We then visually examined the dipole locations and spectra of the ICs. Among the clusters, we observed left and right motor clusters, a fm θ cluster, a left parietal α cluster, and two right parietal α clusters, which we merged into a single cluster. Figure 21 depicts scalp maps, dipole locations, and power spectra for these IC clusters.

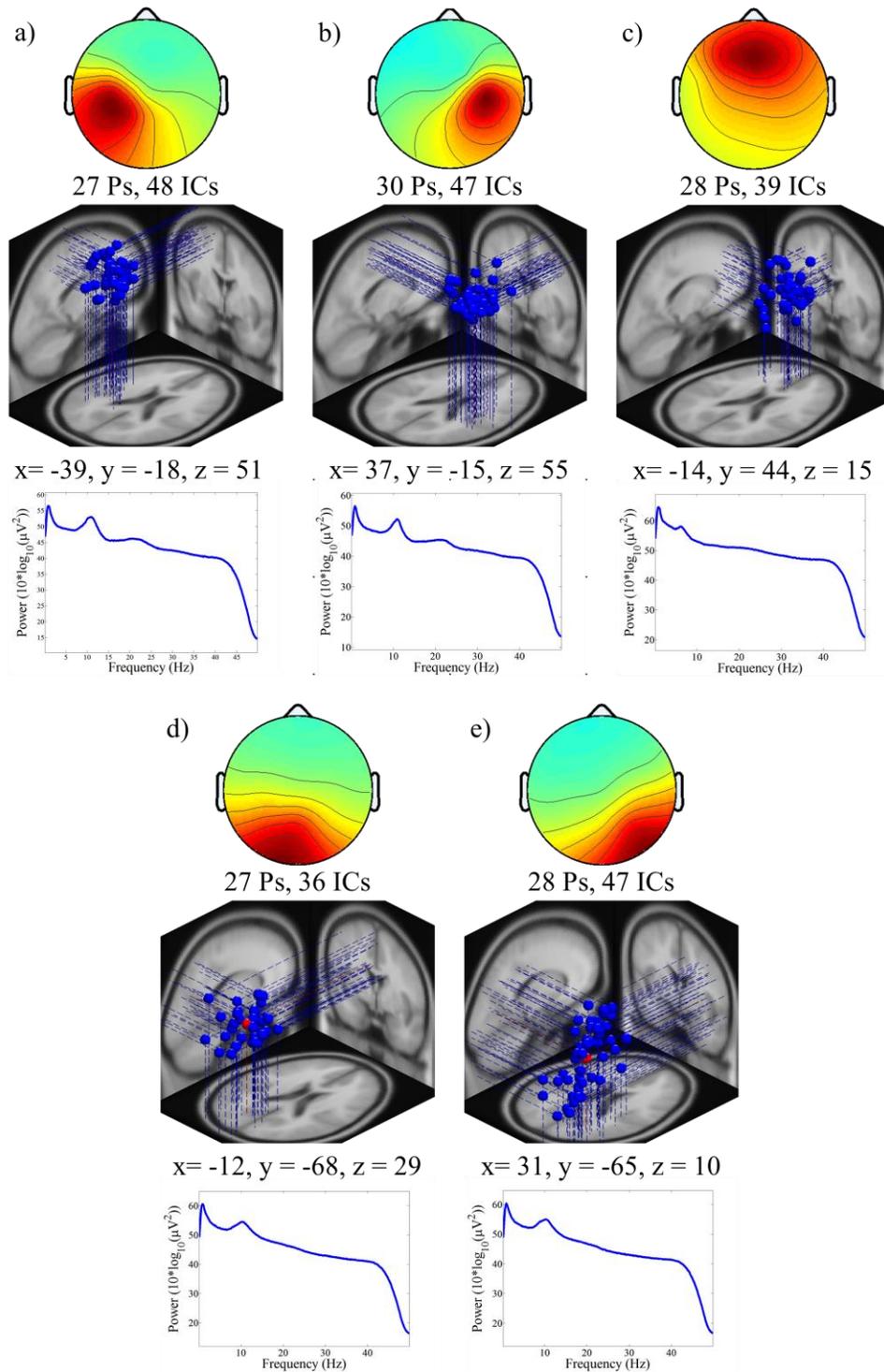


Figure 21. Experiment 3 scalp maps, dipole visualizations, cluster centroid coordinates (Talairach & Tournoux, 1988), and power spectra for IC clusters of interest in Experiment 3 MRT data. From top-left to bottom-right: (a) left motor, (b) right motor, (c) fm θ , (d) left parietal α , (e) right parietal α .

Spectral Power Computation. The following analyses were applied to both artifact-corrected raw EEG and IC activations within the IC clusters of interest. To compute changes in spectral power in the MRT and MI task, we first defined time windows of interest. Time windows are referenced to time 0, which denotes stimulus onset. For the MRT, we analyzed a window initiating at -1558 ms and ending at 4858 ms. For the MI task, the window initiated at -1558 ms and ended at 1858 ms. We used wide windows to accommodate EEGLAB's sliding window power estimation methods which necessarily omit data at the edges of the time window. Baseline spectral power was computed in the [-1000 0] window while trial power was computed in the [0 4300] window for the MRT and in the [0 1300] window for the MI task. Selection of these windows was empirically grounded. First, a long baseline epoch should theoretically lead to more accurate estimation of true baseline activity. Yet, spectral power analysis is highly sensitive to baseline selection and using a long baseline window increases the chance that unwanted artifacts contaminate baseline data (Cohen, 2014; Grandchamp & Delorme, 2011; Hu, Xiao, Zhang, Mouraux, & Ianneti, 2014). Our 1000 ms baseline window balanced these two considerations. Second, we omitted the first 300 ms of the MRT data for two reasons. First, it is well-established that parieto-occipital α power is rapidly suppressed following visual onset of stimuli (Morrell, 1966). This strong suppression would likely contaminate motor-related mu suppression at central electrodes sites. Second previous research suggests that mental rotation processing initiates no earlier than 300 ms post-stimulus onset (Bajric et al., 1999; Heil & Rolke, 2002; Milivojevic

et al., 2011; Milivojevic et al., 2003; Peronnet & Farah, 1989; Riecan sky & Jagla, 2008). For consistency, we omitted the first 300 ms for the MI task as well. The [0 4300] MRT trial window thus contained a full four seconds of data for analysis [300 4300] while the MI task trial window contain one second of data [300 1300]. Third, because the temporal structure of MRT trials was constant during the experiment, participants may have entrained to the trial presentation and engaged in motor preparation prior to the response screen onset. Thus, to prevent potential contamination of EEG data by motor preparation, we excluded the last 700 ms from the MRT trial window.

We conducted time/frequency analysis using EEGLAB's *newtimef* function to detect transient event-related spectral perturbation, or ERSP (Makeig, 1993). We set the lower frequency range of interest to 3 Hz and the upper range to 50 Hz, with 1 Hz increments. To obtain spectral power, for each frequency ($n = 48$) we convolved the EEG/IC signal with Hanning-windowed complex Morlet wavelets (window length = 1115 ms), setting the cycles parameter in EEGLAB to [3 0.5]. This procedure used three cycles at the lowest frequency (3 Hz) and gradually increased the number of cycles as frequency increased, reaching 25 at the highest frequency (50Hz). This technique allows for better frequency resolution at higher frequencies compared to conventional wavelet convolution (Delorme & Makeig, 2004).

Next, we applied single-trial baseline correction to compute mean ERSP for individual trials (Grandchamp & Delorme, 2011). For each trial and frequency *newtimef* outputted 200 complex vectors evenly spaced in time within the entire

5300 ms epoch. We calculated raw spectral power as the squared length of these vectors. Then we divided each power value by the average power (across trials) in the baseline window, yielding 200 power ratios. We then averaged the ratios in the trial window to obtain a mean proportional change in spectral power in the trial window relative to the average baseline window. Finally we log-transformed this proportion, obtaining a log-transformed ERSP that measures change in spectral power in Decibels (dB). This measure is commonly used in EEG time-frequency analysis literature and offers advantages over linearly-scaled measures for parametric inference testing and power visualization (Grandchamp & Delorme, 2011). Using this procedure, we calculated log-ERSPs for each MRT trial for each frequency in our range of interest. We also calculated log-ERSPs in the same manner for the MI task.

Results

Behavioral Results

For the following analyses, we only considered correct responses in the MRT. Overall, participants responded accurately in the MRT (mean percent correct = 90%). Our experimental design, which included a fixed response window (see Figure 18), precluded examination of RT. However, in Experiment 1 we observed an error rate ADE for some trials, with error rates increasing linearly as a function of angular disparity while different trials did not show this pattern (see Figure 4). We examined Experiment 3's behavioral data for the presence of a similar error rate ADE. We conducted repeated measures analysis of variance (ANOVA) on error rates, with Greenhouse-Geisser correction in the case of

sphericity violations (Geisser & Greenhouse, 1958), denoted by F_{GG} . We submitted error rates to a 2 (trial type: same, different) x 7 (angular disparity: 0°, 30°, 60°, 90°, 120°, 150°, 180°) ANOVA. This analysis revealed a positive linear relationship between angular disparity and error rate (i.e. an error rate ADE), $F_{GG}(3.50,108.39) = 16.76, p < .001, \eta_p^2 = .351$. This main effect was qualified by a two-way trial type x angular disparity interaction, $F_{GG}(4.19,129.98) = 13.48, p < .001, \eta_p^2 = .303$. As shown in Figure 22, same trial error rates increased linearly concomitant with angular disparity but remained static for different trials. Follow-up Bonferroni-corrected ANOVAs within each trial type ($\alpha_{critical} = 0.025$) confirmed an ADE for same, $F_{GG}(2.95,91.57) = 25.46, p < .001, \eta_p^2 = .451$, but not different trials, $F_{GG}(4.31,133.55) = 1.21, p > .1$. Thus, the pattern of error rate data in Experiment 1 was replicated in Experiment 3.

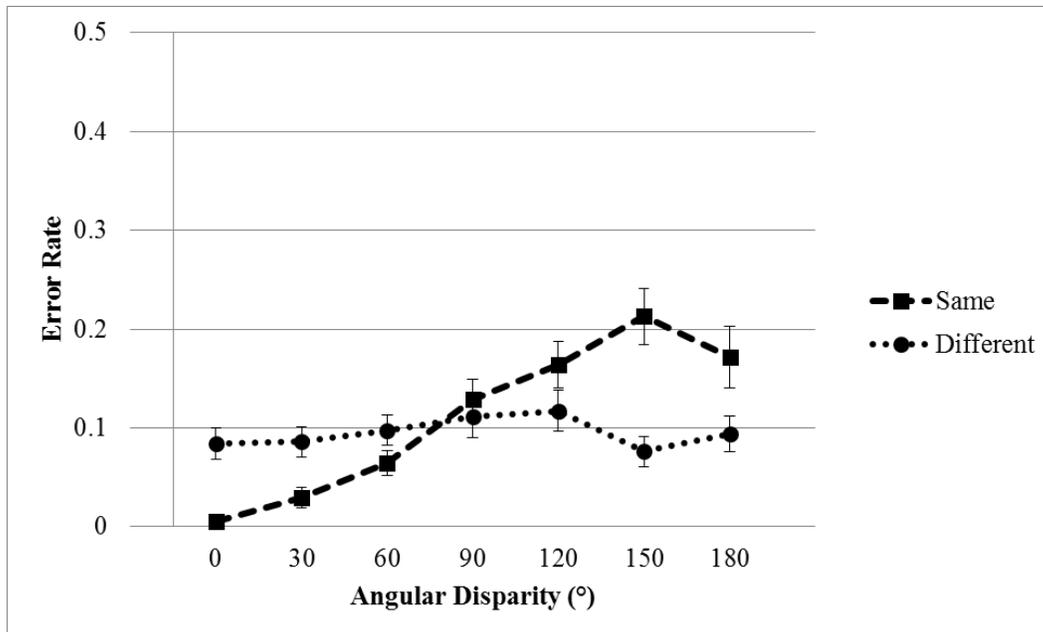


Figure 22. Experiment 3 mean error rate as a function of angular disparity and trial type for the MRT. Error bars show standard errors.

EEG Results –Electrode Analyses

Prior to analyzing the MRT data, we first computed mean log-ERSPs separately at sensorimotor (C3 & C4) and parietal electrodes (P3 & P4) for the MI task. The goal here was to determine for each participant which frequency in the upper α -band (11 – 13 Hz) maximally elicited mu suppression in the MI task. We refer to this personalized frequency as the individual α frequency or IAF. It is important to note that mu suppression in the MI task is highly lateralized with maximal suppression occurring over the hemisphere contralateral to the imagined hand (Osuagwu & Vuckovic, 2014). Therefore, we computed IAFs for left-lateralized and right-lateralized electrodes separately, using MI task data from right and left hand trials, respectively. We note that for one participant C4 was removed during MI task preprocessing. For this participant we entered the middle of the upper α range (12 Hz) as their IAF. Overall the mean IAF for sensorimotor electrodes was 11.7 Hz for C3, 11.4 Hz for C4, and 11.4 Hz for both parietal electrodes.

Prior to analysis we collapsed data across hemispheres. We made this decision for two reasons. First, the right and left response buttons were always mapped to the same responses (“same” and “different,” respectively). Consequently, motor preparation for the behavioral response, if present, would differentially impact EEG power at different electrodes. Second, while motor imagery for hand actions is lateralized (Osuagwu & Vuckovic, 2014; Pfurtscheller et al., 2000), cognitive processing in the MRT depends on broad bilateral cortical networks (Carpenter et al., 1999; Jordan, Heinze, Lutz, Kanowski, & Jäncke,

2001; Sack et al., 2008; Sack & Schuhmann, 2012; Tomasino & Gremese, 2015; Zacks, Vettel, & Michelon, 2003; Zacks, 2008). For these reasons, we elected to investigate EEG power bilaterally in the present experiment.

We also removed outliers prior to analysis. Single-trial baseline corrected log-ERSPs are prone to positively-skewed distributions due to outliers (Grandchamp & Delorme, 2011). Our outlier removal procedure involved omitting the largest and smallest log-ERSP value for each participant within each level of angular disparity. Such outlier trimming methods have been shown to be superior to traditional ± 3 -SD elimination (Bush, Hess, & Wolford, 1993).

Bilateral Sensorimotor Electrode Analysis. Using our trimming procedure, we removed 7.5% of the data prior to analysis. We subsequently used R (R Development Core Team, 2014) to conduct linear mixed-model analysis with the lme4 (Bates et al., 2014) and lmerTest (Kuznetsova et al., 2014) packages. We first entered log-ERSP as the dependent variable in the LMM. Then we entered grand-mean centered angular disparity, trial type (same vs. different), and their interaction as fixed effects into the model. VIF was < 4 for all of the model's fixed effects. We determined the random effects structure of the model using Experiment 2's iterative procedure. As a result, we included random angular disparity slopes and intercepts for participants, omitting item-related random effects.

Figures 23 and 24 depict the log-ERSP data contributing to this analysis and Table 8 presents the coefficients of the model. Log-ERSP was significantly less than zero, as indicated by the significant negative β coefficient for the model

intercept. Thus, mu suppression was observed. The analysis revealed a main effect of angular disparity, $F(1,31.6) = 56.79, p < .001$. Increasing angular disparity was associated with decreasing mu suppression. There was also a main effect of trial type, $F(1,5485.1) = 546.77, p < .001$. Participants suppressed mu more for same vs. different trials. These main effects were qualified by an angular disparity x trial type interaction, $F(1,5485.1) = 309.55, p < .001$. Follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) confirmed that for same trials, mu suppression decreased linearly as angular disparity increased, $F(1,34.79) = 104.29, p < .001$. In contrast, mu suppression for different trials did not vary due to angular disparity, $F(1,43.82) = 1.91, p > .1$.

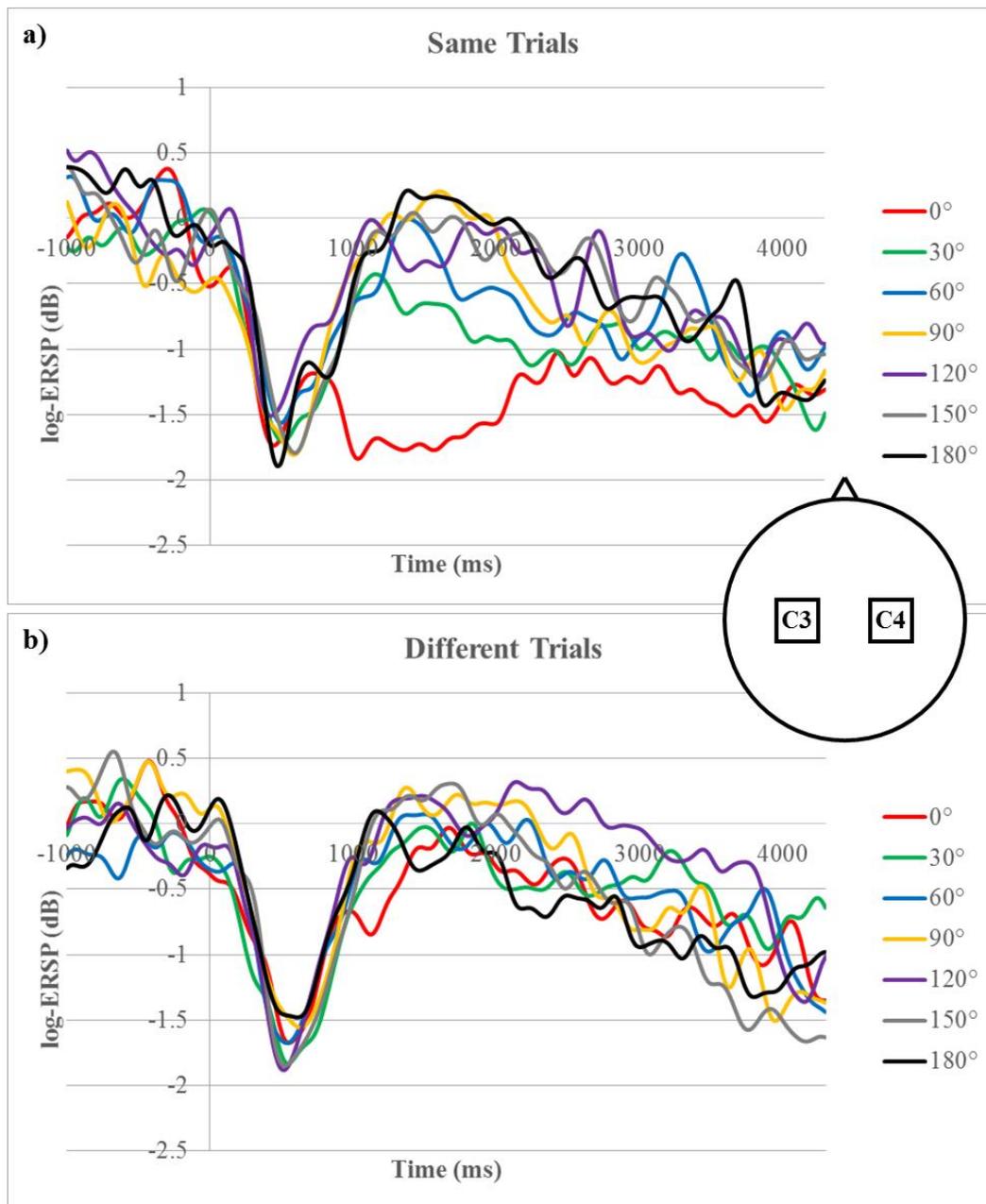


Figure 23. Experiment 3 mean log-ERSP in the MRT collapsed across C3 and C4 (IAF \pm 1Hz). Log-ERSPs are plotted from -1000 to +4300 ms relative to stimulus onset as a function of angular disparity for same (a) and different (b) trials.

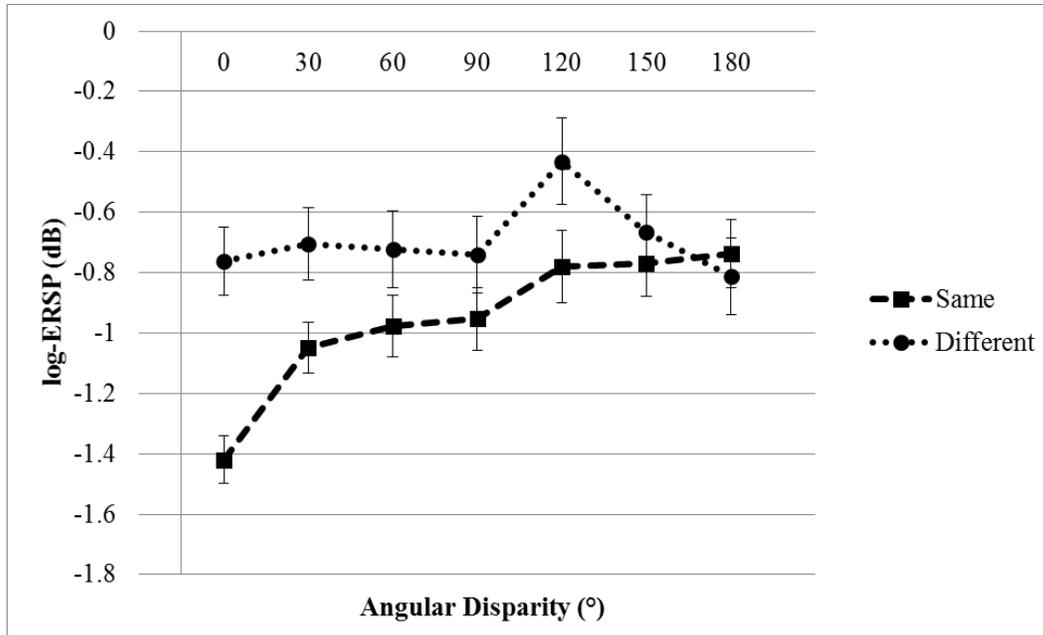


Figure 24. Experiment 3 mean log-ERSP (C3 & C4, IAF \pm 1Hz) as function of angular disparity and trial type in the MRT. Error bars show standard errors.

Table 8. Experiment 3 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log-ERSP (C3 & C4, IAF \pm 1Hz) in the MRT as a function of angular disparity and trial type (same = 1, different = 0).

	Coef. β	SE(β)	df	<i>t</i>
(Intercept)	-7.54e-01	9.45e-02	3.10e+01	-7.98 ***
grand-mean centered				
angular disparity	2.20e-04	2.47e-04	4.10e+01	0.89
trial type	-2.44e-01	1.04e-02	5.49e+03	-23.38 ***
grand-mean centered				
angular disparity x				
trial type	3.05e-03	1.73e-04	5.49e+03	17.60 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Bilateral Parietal Electrode Analysis. 7.5% of the data were trimmed prior to analysis. We conducted the same linear mixed-model analysis on mean MRT log-ERSP within the 300 – 4300 ms post-stimulus onset time window. VIF was < 4 for all of the model’s fixed effects. We then applied our iterative procedure to determine each LMM’s random effects structure. As a result, we

included random angular disparity slopes and intercepts for participants, omitting item-related random effects.

Figures 25 and 26 depict the log-ERSP data contributing to this analysis and Table 9 presents the coefficients of the model. Log-ERSP was significantly less than zero, as indicated by the significant negative β coefficient for the model intercept. Thus, parietal α suppression was observed. The analysis revealed a main effect of angular disparity, $F(1,34.7) = 35.31, p < .001$. Increasing angular disparity was associated with increasing parietal α suppression. There was also a main effect of trial type, $F(1,5485.5) = 8.09, p < .01$. Parietal α suppression was greater for different vs. same trials. The angular disparity x trial type interaction was not significant, $F(1,5485.3) = 2.32, p > .1$.

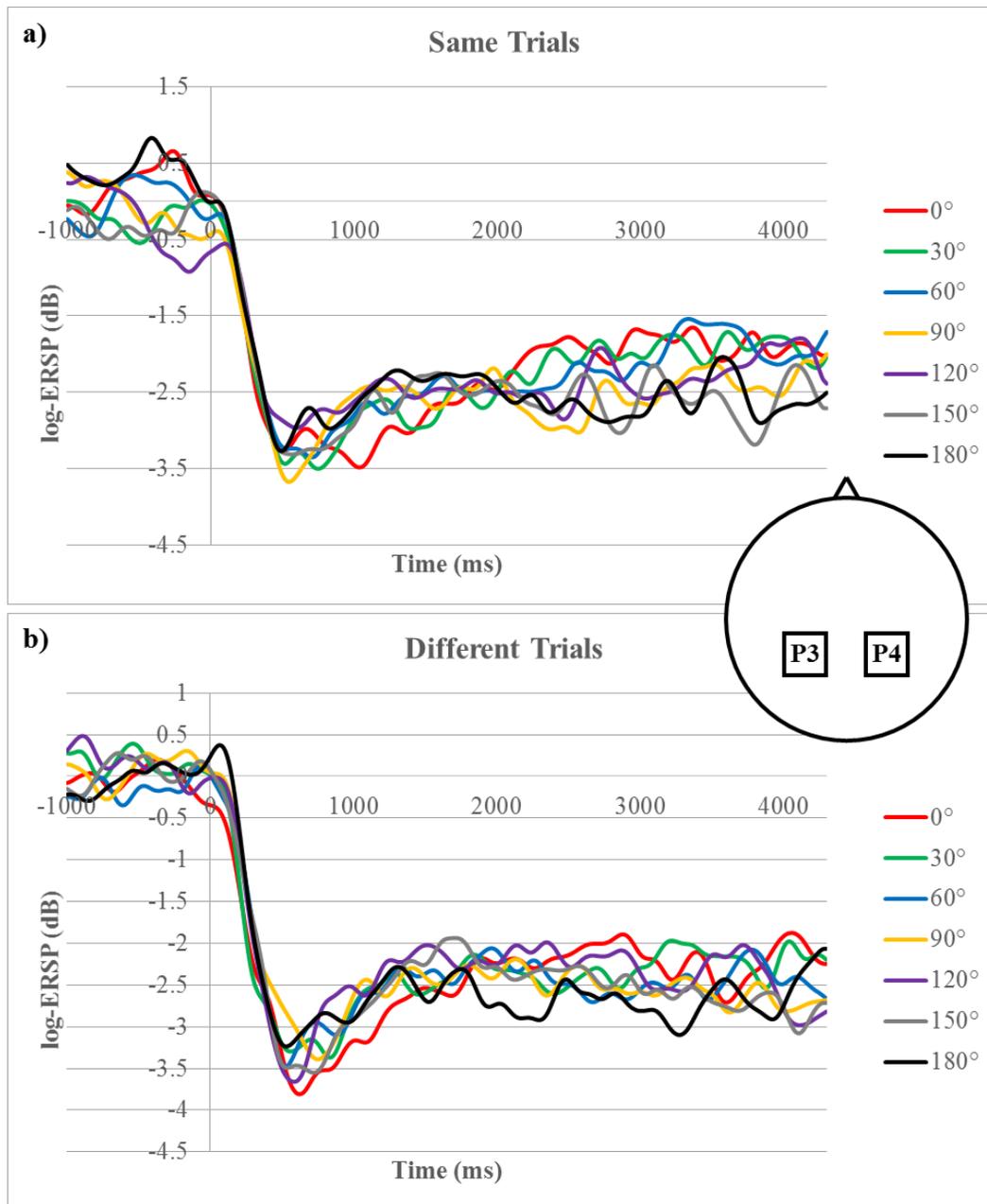


Figure 25. Experiment 3 mean log-ERSP in the MRT collapsed across P3 and P4 (IAF \pm 1Hz). Log-ERSPs are plotted from -1000 to +4300 ms relative to stimulus onset as a function of angular disparity for same (a) and different (b) trials.

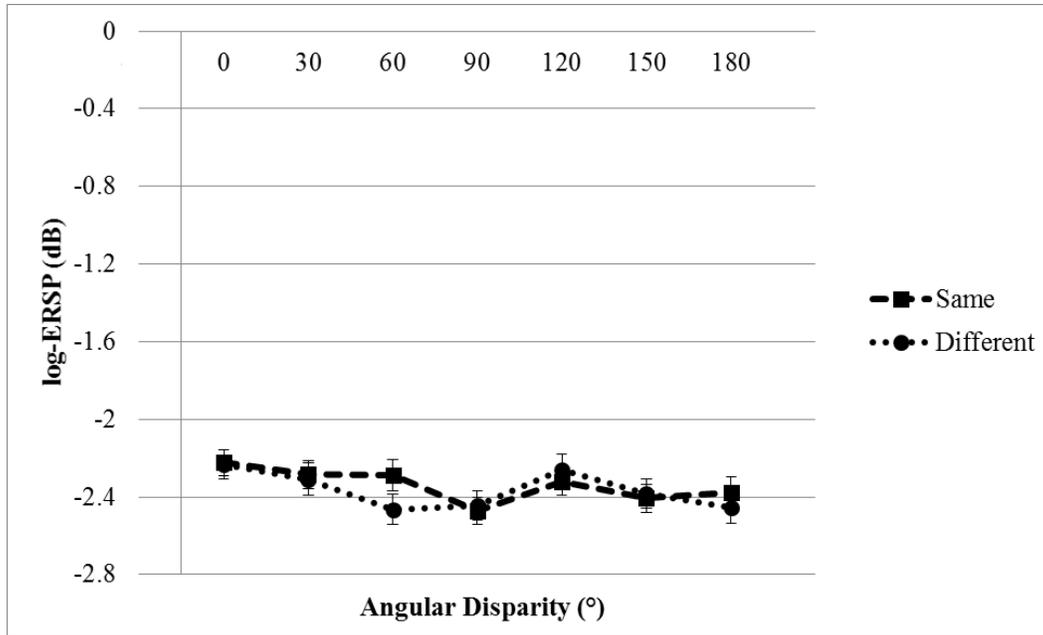


Figure 26. Experiment 3 mean log-ERSP (P3 & P4, IAF \pm 1Hz) as function of angular disparity and trial type in the MRT. Error bars show standard errors.

Table 9. Experiment 3 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log-ERSP (P3 & P4, IAF \pm 1Hz) in the MRT as a function of angular disparity and trial type (same = 1, different = 0).

	Coef. β	SE(β)	df	t
(Intercept)	-2.36e+00	4.48e-02	3.20e+01	-52.70 ***
grand-mean centered				
angular disparity	-9.46e-04	1.61e-04	6.20e+01	-5.89 ***
trial type	-2.69e-02	9.45e-03	5.49e+03	-2.85 ***
grand-mean centered				
angular disparity x				
trial type	2.40e-04	1.57e-04	5.49e+03	1.52

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

EEG Results –Independent Component Analyses

We next examined the IC clusters that we extracted previously. These included two lateralized motor clusters with characteristic mu spectra, a frontal midline theta ($fm\theta$) cluster, and two lateralized parietal α clusters (see Figure 21). As with the electrode analysis, we collapsed data from complementary lateralized

IC clusters prior to analysis. This resulted in one bilateral motor cluster, the fm θ cluster, and one bilateral parietal α cluster. It is also important to note that participants' ICs varied and some participants did not contribute ICs to certain clusters. However, for all clusters the majority of participants contributed one or more ICs (bilateral motor: $n = 30$, fm θ : $n = 28$, bilateral parietal α : $n = 32$).

In the following sections, we conducted the same linear mixed-model analysis on mean MRT log-ERSP within the 300 – 4300 ms post-stimulus onset time window for each IC cluster. In contrast to the electrode analysis, we did not compute IAFs from the MI task and instead used an appropriate frequency band for each cluster (bilateral motor and parietal: 11 – 13Hz, fm θ : 5 – 7 Hz). This decision was based on the variably observed comparable ICs within participants in the MI task and MRT task due to their different task demands. As before, prior to analysis we trimmed outliers for each cluster (% trials removed: bilateral motor – 7.5%, fm θ – 7.6%, bilateral parietal – 7.5%) and confirmed VIF < 4 for each model's fixed effects. We then applied our iterative procedure to determine each LMM's random effects structure. In all cases we included random angular disparity slopes and intercepts for participants, omitting item-related random effects.

Bilateral Motor IC Analysis. Figures 27 and 28 depict the log-ERSP (11 – 13 Hz) data contributing to this analysis and Table 10 presents the coefficients of the model. Log-ERSP was significantly *greater* than zero, as indicated by the significant positive β coefficient for the model intercept. Thus, in contrast to the electrode analysis, mu *enhancement* was observed. There was a main effect of

angular disparity, $F(1,40.8) = 1215.7, p < .001$. Increasing angular disparity was associated with decreasing motor IC mu suppression. There was also a main effect of trial type, $F(1,5155.7) = 2987.6, p < .001$. Participants suppressed mu more for same vs. different trials. These main effects were qualified by an angular disparity x trial type interaction, $F(1,5155.4) = 1284.8, p < .001$. Follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) confirmed that for same trials mu suppression decreased linearly as angular disparity increased, $F(1,34.92) = 1459.7, p < .001$. Mu suppression decreased linearly for different trials as well but at a slower rate, $F(1,2327.4) = 75.31, p < .001$.

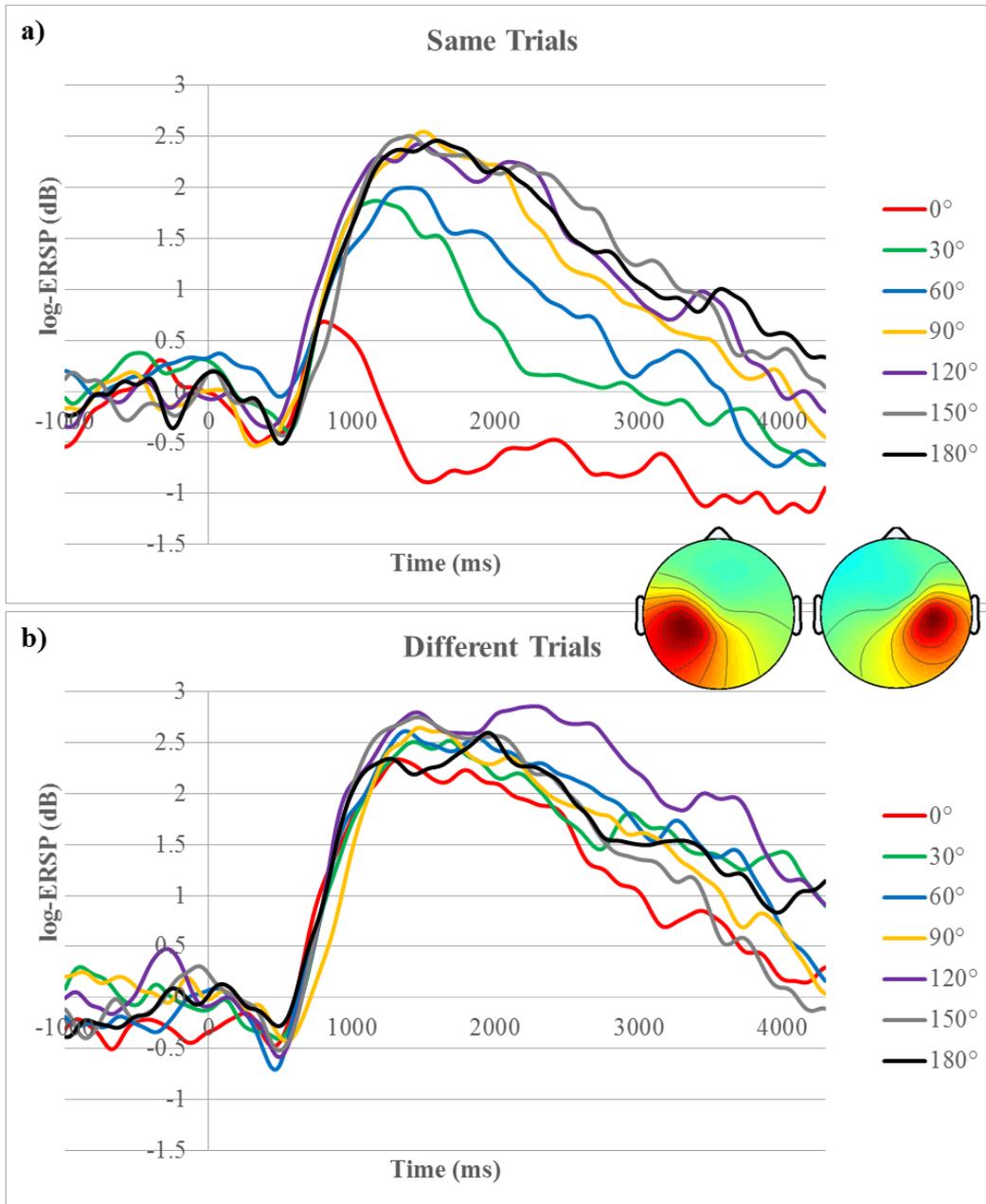


Figure 27. Experiment 3 mean log-ERSP in the MRT collapsed across L & R motor ICs (11 – 13 Hz). Log-ERSPs are plotted from -1000 to +4300 ms relative to stimulus onset as a function of angular disparity for same (a) and different (b) trials.

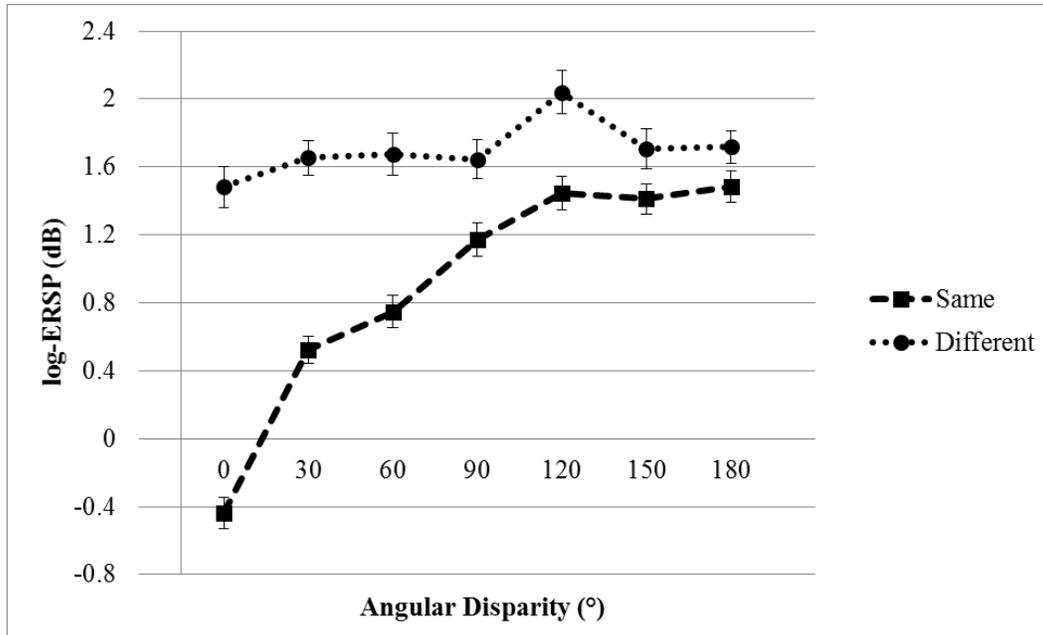


Figure 28. Experiment 3 mean log-ERSP (L & R motor IC, 11 – 13 Hz) as a function of angular disparity and trial type in the MRT. Error bars show standard errors.

Table 10. Experiment 3 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log-ERSP (left & right motor IC) in the MRT as a function of angular disparity and trial type (same = 1, different = 0).

	Coef. β	SE(β)	df	<i>t</i>
(Intercept)	1.65e+00	5.85e-02	3.00e+01	28.22 ***
grand-mean centered				
angular disparity	1.40e-03	2.04e-04	9.50e+01	6.88 ***
trial type	-7.96e-01	1.46e-02	5.12e+03	-54.66 ***
grand-mean centered				
angular disparity x				
trial type	8.68e-03	2.42e-04	5.12e+03	35.84 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Fm θ IC Analysis. Figures 29 and 30 depict the log-ERSP (5 – 7 Hz) data contributing to this analysis and Table 11 presents the coefficients of the model. Log-ERSP was significantly greater than zero, as indicated by the significant positive β coefficient for the model intercept. Thus, fm θ power enhancement was

observed. There was a main effect of angular disparity, $F(1,33.8) = 272.64, p < .001$. Increasing angular disparity was associated with increasing fm θ power. There was also a main effect of trial type, $F(1,4712.3) = 110.84, p < .001$. Different trials elicited higher fm θ power than same. These main effects were qualified by an angular disparity x trial type interaction, $F(1,4711.8) = 258.29, p < .001$. Follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) confirmed that for same trials fm θ power linearly increased concomitant with angular disparity, $F(1,43.46) = 527.95, p < .001$. Fm θ power increased linearly for different trials as well but at a slower rate, $F(1,41.74) = 21.74, p < .001$.

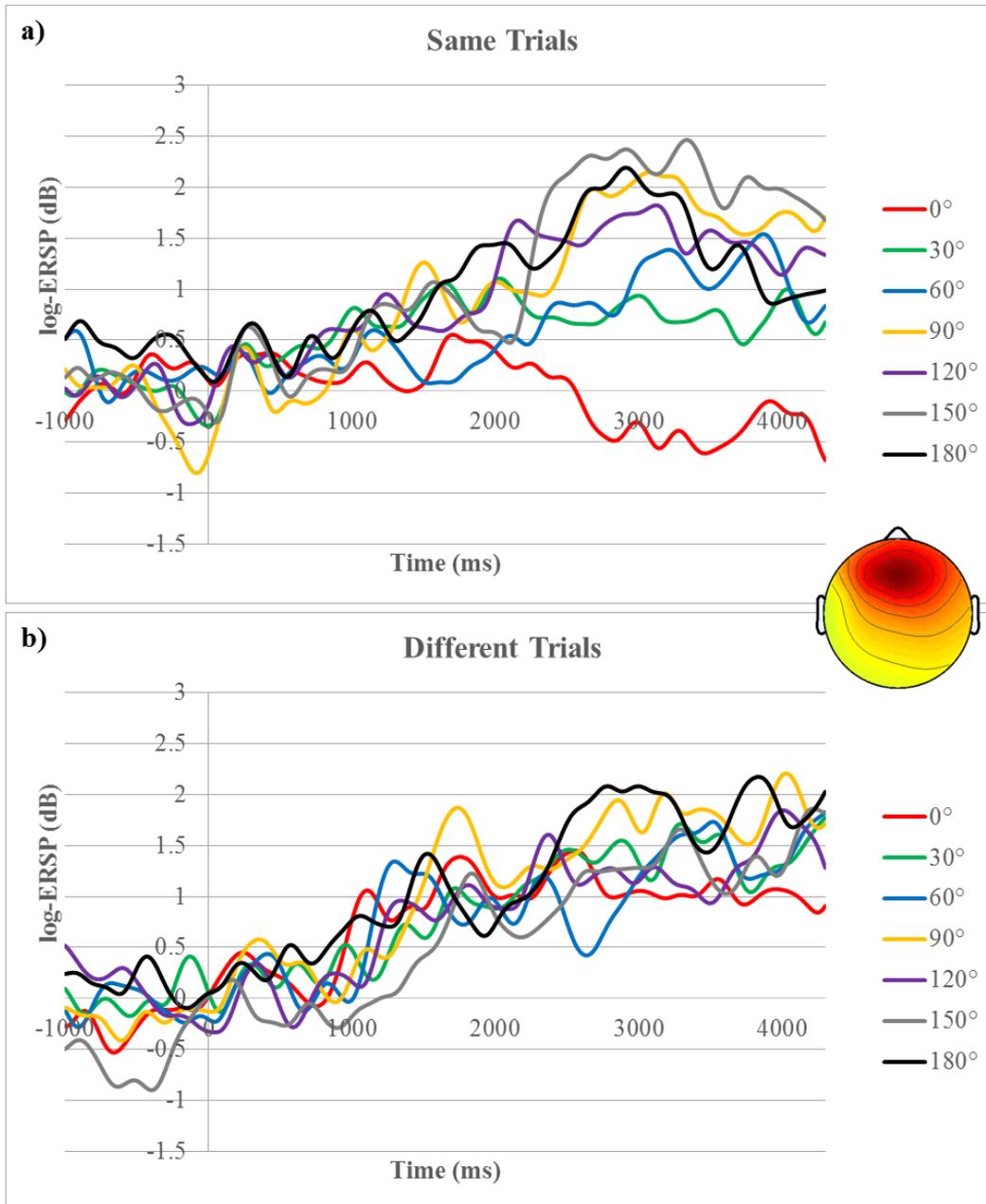


Figure 29. Experiment 3 mean log-ERSP in the MRT for the fm θ IC (5 – 7 Hz). Log-ERSPs are plotted from -1000 to +4300 ms relative to stimulus onset as a function of angular disparity for same (a) and different (b) trials.

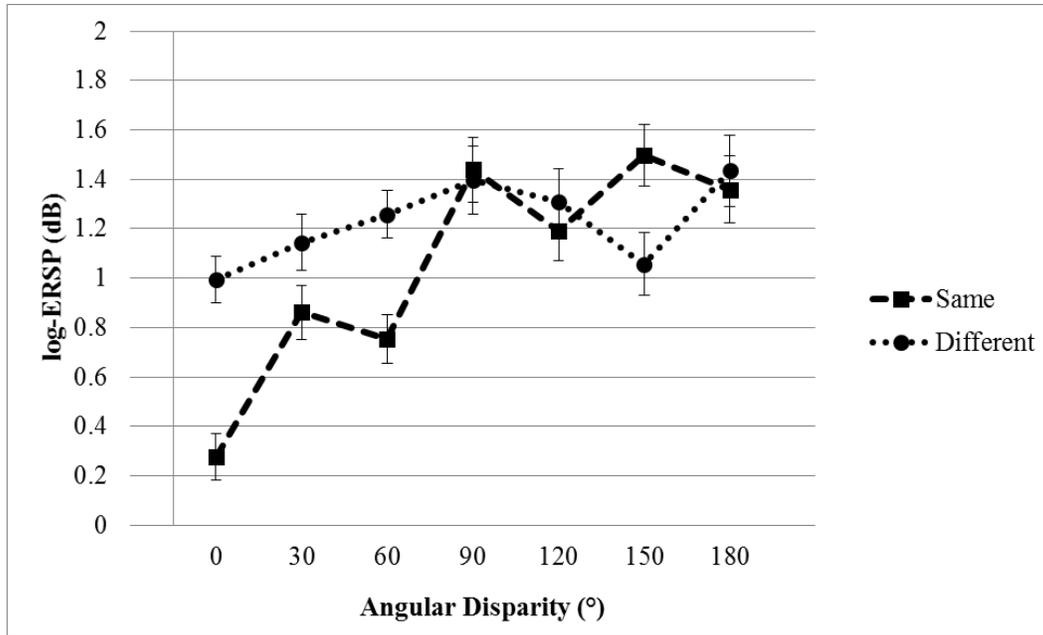


Figure 30. Experiment 3 mean log-ERSP (fmθ IC, 5 – 7 Hz) as a function of angular disparity and trial type in the MRT. Error bars show standard errors.

Table 11. Experiment 3 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log-ERSP (fmθ IC) in the MRT as a function of angular disparity and trial type (same = 1, different = 0).

	Coef. β	SE(β)	df	<i>t</i>
(Intercept)	1.18e+00	5.08e-02	2.90e+01	23.215 ***
grand-mean centered				
angular disparity	1.25e-03	2.59e-04	6.90e+01	4.82 ***
trial type	-1.83e-01	1.74e-02	4.71e+03	-10.53 ***
grand-mean centered				
angular disparity x				
trial type	4.66e-03	2.90e-04	4.71e+03	16.07 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Bilateral Parietal α IC Analysis. Figures 31 and 32 depict the log-ERSP (11 – 13 Hz) data contributing to this analysis and Table 12 presents the coefficients of the model. Log-ERSP was significantly less than zero, as indicated by the significant negative β coefficient for the model intercept. Thus, parietal α suppression was observed. There was a main effect of angular disparity, $F(1,36.2)$

= 74.13, $p < .001$. Increasing angular disparity was associated with increasing parietal α suppression. There was also a main effect of trial type, $F(1,5485.2) = 303.12$, $p < .001$. Parietal α suppression was greater for different vs. same trials. These main effects were qualified by an angular disparity x trial type interaction, $F(1,5485.1) = 100.73$, $p < .001$. Follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) confirmed that for same trials parietal α suppression increased linearly concomitant with angular disparity, $F(1,33.73) = 77.82$, $p < .001$. Parietal α suppression increased linearly for different trials as well but at a slower rate, $F(1,753.85) = 7.58$, $p < .01$.

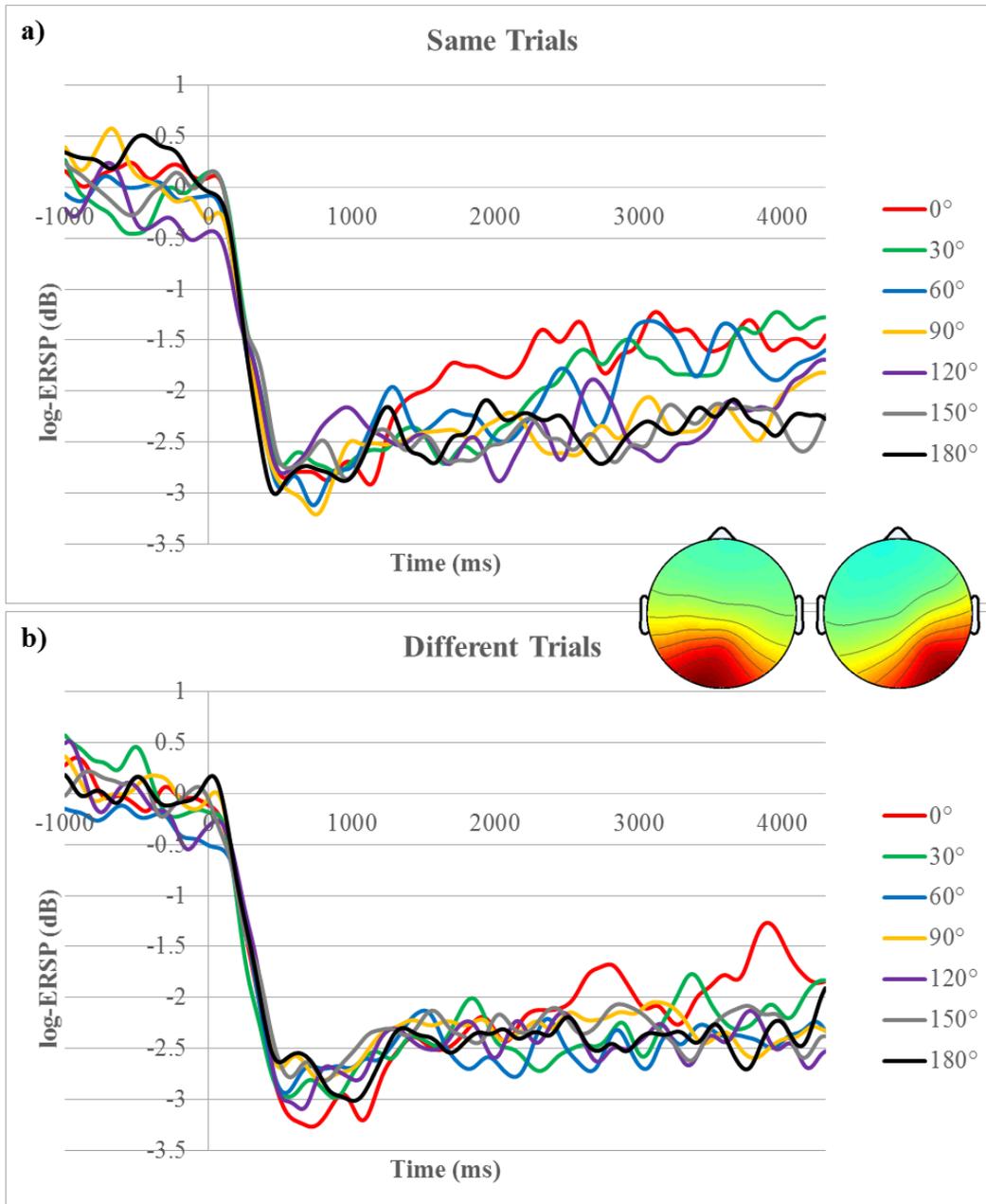


Figure 31. Experiment 3 mean log-ERSP in the MRT collapsed across L & R parietal α ICs (11 – 13 Hz). Log-ERSPs are plotted from -1000 to +4300 ms relative to stimulus onset as a function of angular disparity for same (a) and different (b) trials.

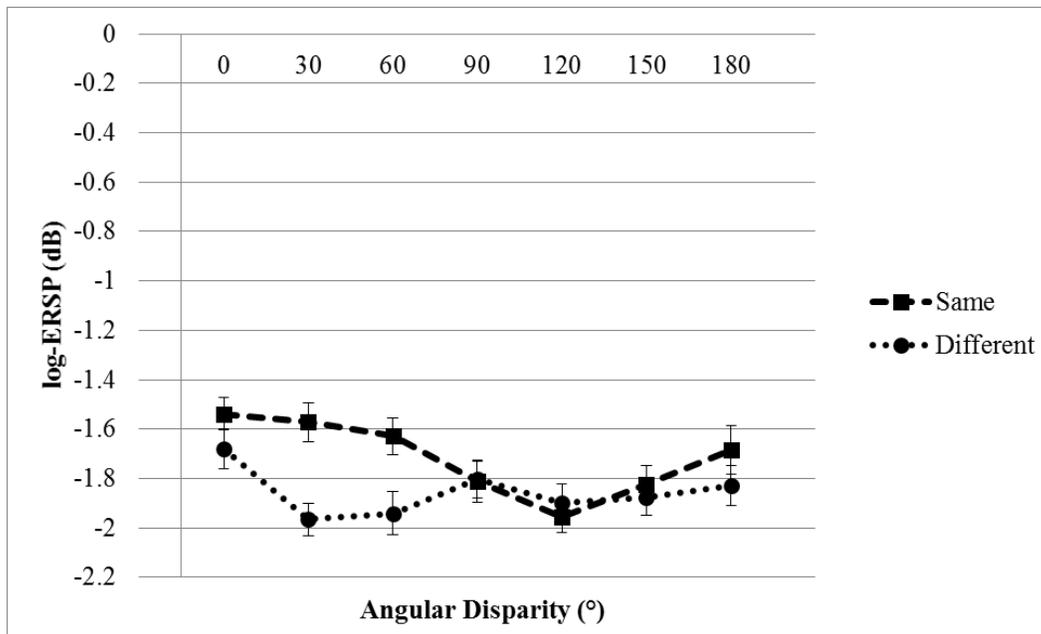


Figure 32. Experiment 3 mean log-ERSP (parietal α IC, 11 – 13 Hz) as a function of angular disparity and trial type in the MRT. Error bars show standard errors.

Table 12. Experiment 3 coefficient estimates (β), standard errors SE (β), degrees of freedom, and associated t-values ($=\beta/SE(\beta)$) for the linear mixed-model predicting log-ERSP (parietal α IC) in the MRT as a function of angular disparity and trial type (same = 1, different = 0).

	Coef. β	SE(β)	df	<i>t</i>
(Intercept)	-1.88e+00	5.96e-02	3.10e+01	-31.63 ***
grand-mean centered				
angular disparity	-2.61e-04	1.30e-04	6.90e+01	-2.01 ***
trial type	-1.44e-01	8.26e-03	5.49e+03	17.41 ***
grand-mean centered				
angular disparity x				
trial type	-1.38e-03	1.37e-04	5.49e+03	-10.04 ***

⁺ $p > .05$, * $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Individual Differences – log-ERSP

We next considered how inter-participant individual differences (see Table 7) influenced log-ERSP. Experiment 2’s findings suggested influences of gender, video game experience, and spatial ability / self-confidence on strategy use in the

MRT. Thus in Experiment 3 we focused our investigation on these factors. In addition we examined the influence of motor imagery vividness as measured by the VMIQ-2 (Roberts et al., 2008) which was newly added in Experiment 3. Several of these measures were highly inter-correlated and so we conducted principle components analysis (varimax rotation) on the measures, dummy coding gender (0 = male, 1 = female) as before. This procedure yielded three factor scores. Table 13 presents the extracted components and their factor loadings and Table 14 presents the factor loadings for the components whose eigenvalues exceeded 1. Based on the factor loadings we interpreted each component as follows: spatial ability /self-confidence (1), motor imagery vividness (2), and gender / video game experience (3). We then included these factor scores in the mixed-models from the previous analyses.

Table 13. Extracted components, eigenvalues, and % variance explained from principle components analysis of Experiment 3 individual difference measures of interest.

Component	Initial Eigenvalues	
	Total	% of Variance
1	3.52	39.12
2	1.83	20.37
3	1.10	12.25
4	0.86	9.52
5	0.75	8.38
6	0.47	5.21
7	0.27	2.99
8	0.13	1.44
9	0.06	0.72

Table 14. Factor loadings of extracted components from principle components analysis of Experiment 2 individual difference measures of interest. Maximally-loaded measures are bolded for each component and interpretations based of loadings are italicized.

Measure	Component 1 <i>Spatial Ability/ Self-Confidence</i>	Component 2 <i>Motor Imagery Vividness</i>	Component 3 <i>Gender/ VG Exp</i>
Gender	-0.37	0.00	-0.75
SBSODS	0.88	0.1	0.29
FRS _{self_confidence}	0.88	0.06	0.02
FRS _{survey_strategy}	0.85	0.11	-0.02
FRS _{knowledge_cardinal}	0.60	0.04	0.44
Video game exp	-0.05	0.20	0.75
VMIQ-2 _{Kinesthetic}	0.11	0.92	-0.05
VMIQ-2 _{Internal}	0.29	0.87	0.12
VMIQ-2 _{External}	-0.09	0.67	0.20

Electrode log-ERSP. To examine individual differences in the electrode data we reused the previous LMMs predicting bilateral central and parietal electrode log-ERSP. We entered the factor scores into the models as additional fixed effects, both as main effects and interactions with angular disparity and trial type but did not include interactions between the factor scores. We noted that some of the models' fixed effects possessed $VIF > 4$ (but < 10). This observation was likely due to the several interaction terms in the models and should not be interpreted as cause for concern. Based on our iterative procedure, both models included random angular disparity slopes and intercepts for participants in their random effects structures, omitting item-related effects. In cases where the gender / video game experience factor yielded significant effects we describe these findings referencing gender. However, it is important to note that gender and video game experience were marginally anti-correlated, $r(30) = -.33, p = .07$.

Therefore, any observed gender effects may in fact stem from differential video game experience.

Bilateral Sensorimotor Electrodes. This analysis revealed a main effect of gender / video game experience, $F(1,25.4) = 6.58, p = .02$. Females overall suppressed μ more than males. This main effect was qualified by two-way interactions with both angular disparity, $F(1,26.6) = 4.44, p = .04$, and trial type, $F(1,5477.0) = 85.89, p < .001$, and a three-way interaction, $F(1,5476.9) = 9.43, p < .01$. Figure 33 depicts the data underlying these interactions, categorically split by gender. We subsequently ran follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$). For same trials, μ suppression decreased linearly as angular disparity increased, $F(1,28.28) = 110.16, p < .001$, and females suppressed μ more than males, $F(1,27.85) = 6.02, p = .02$. Further as angular disparity increased, μ suppression decreased more rapidly for males than females, $F(1,28.39) = 5.87, p = .02$. For different trials, μ suppression did not vary as a function of angular disparity, $F(1,40.70) = 1.98, p > .1$, and females suppressed μ more than males, $F(1,28.02) = 7.70, p < .01$. In contrast to same trials, different trial μ suppression did not vary with angular disparity for both genders, $F(1,43.66) = 1.43, p > .1$. No other individual difference main effects or interactions emerged.

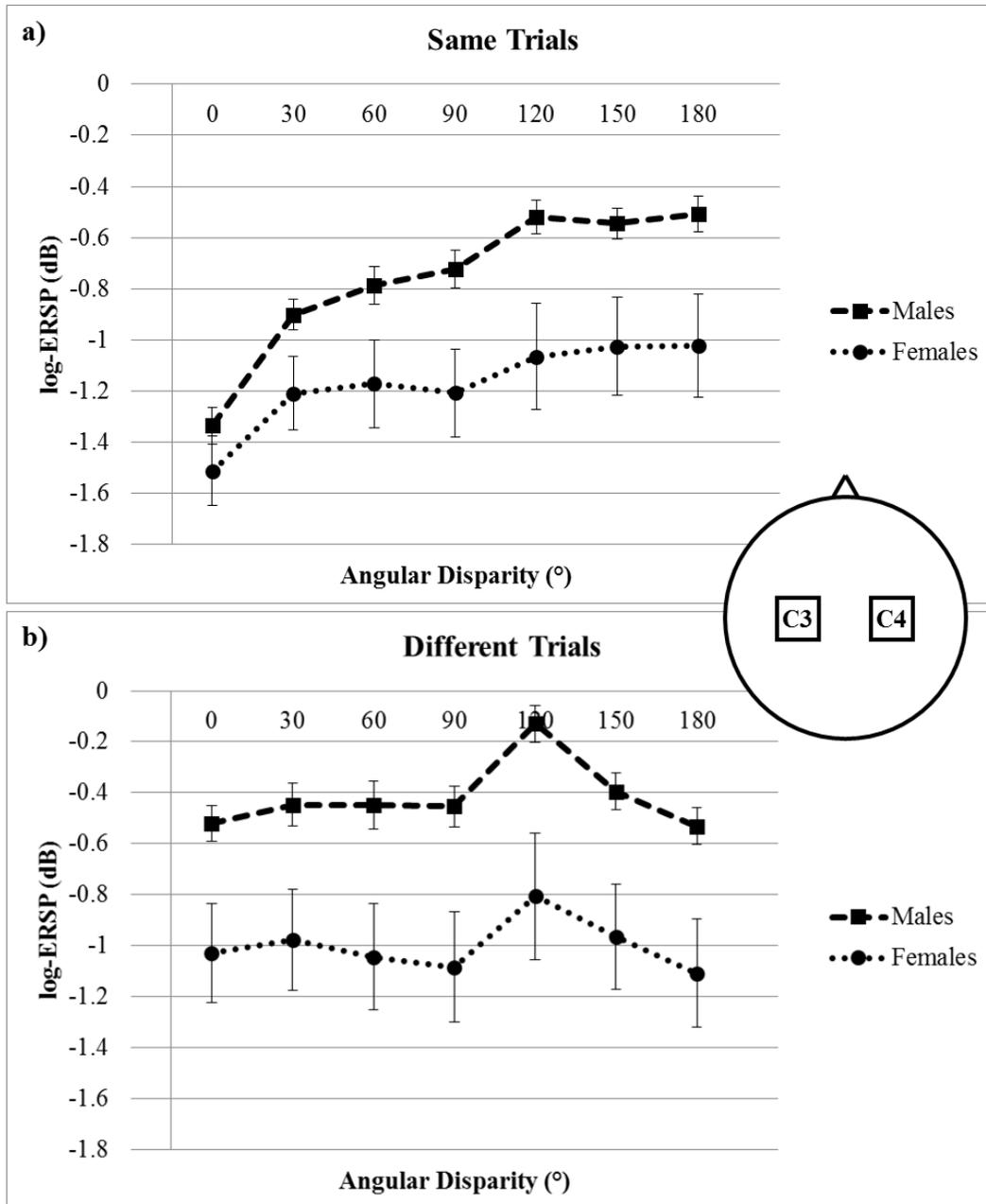


Figure 33. Experiment 3 mean log-ERSP in the MRT collapsed across C3 and C4 (IAF \pm 1Hz). Data are averaged within [+300 ms +4300 ms] time window (relative to stimulus onset) as a function of angular disparity and gender for same (a) and different (b) trials. Error bars show standard errors.

Bilateral Parietal Electrodes. This analysis revealed a gender / video game experience x angular disparity interaction, $F(1,32.8) = 4.66, p = .04$. Parietal α suppression increased concomitant with angular disparity more steeply for females than males. There was also a gender / video game experience x trial type interaction, $F(1,5476.7) = 18.21, p < .001$. Parietal α suppression for different trials was greater for females than males but equivalent for same trials. Figure 34 depicts the data underlying these interactions, categorically split by gender. We note, however, that follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) did not yield main effects of gender / video game experience (all p 's $> .1$). No other individual difference main effects or interactions emerged.

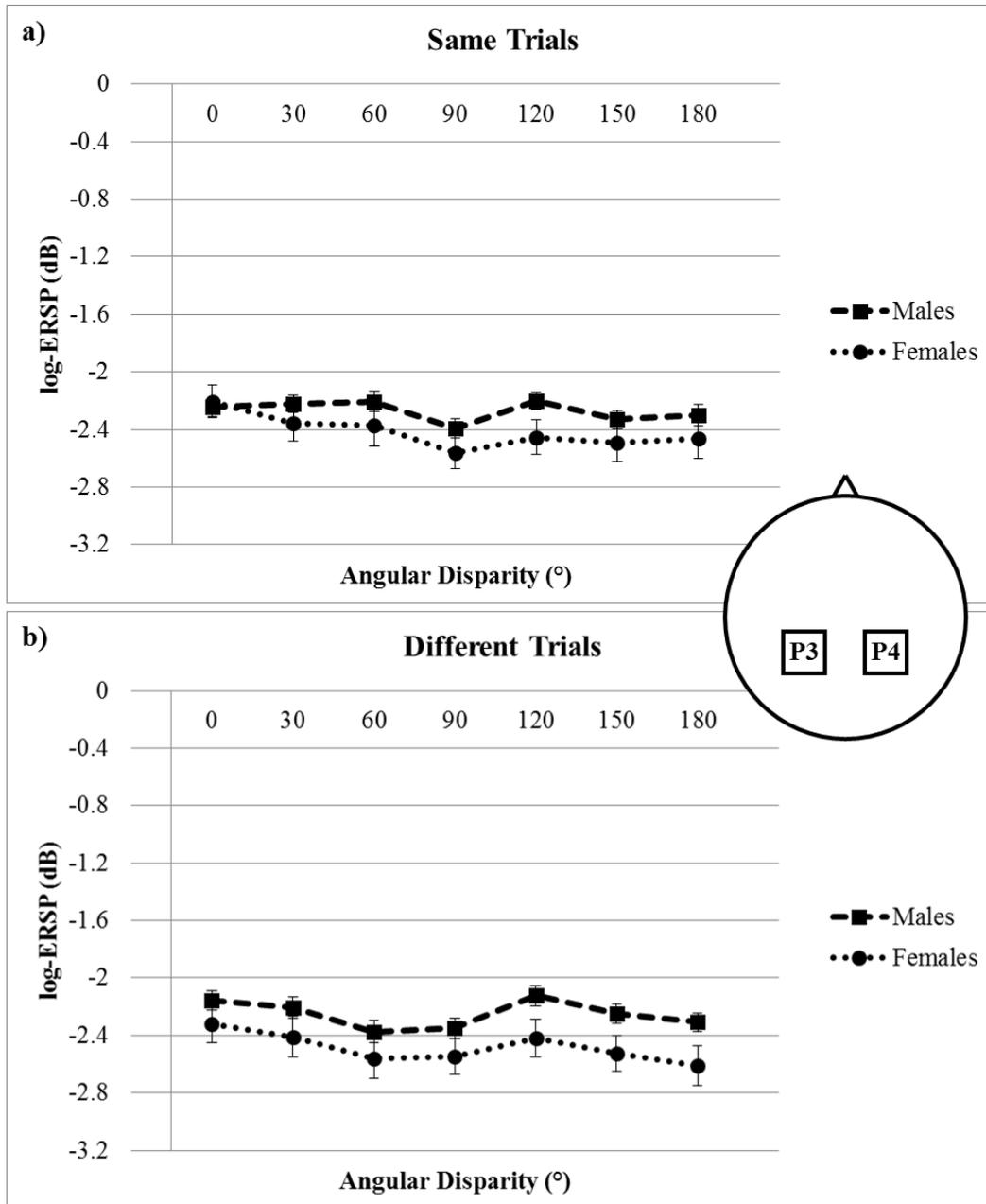


Figure 34. Experiment 3 mean log-ERSP in the MRT collapsed across P3 and P4 (IAF \pm 1Hz). Data are averaged within [+300 ms +4300 ms] time window (relative to stimulus onset) as a function of angular disparity and gender for same (a) and different (b) trials. Error bars show standard errors.

IC Cluster log-ERSP. We next examined the influence of individual differences on the IC data. For each IC cluster we reused the previous LMM predicting log-ERSP and entered the factor scores in the same manner as in the electrode analysis. VIF was < 4 for each model's fixed effects. We then applied our iterative procedure to determine each LMM's random effects structure. In all cases we included random angular disparity slopes and intercepts for participants, omitting item-related random effects. As before, in cases where the gender / video game experience factor yielded significant effects we describe these findings referencing gender.

Bilateral Motor IC. This analysis revealed a main effect of gender / video game experience, $F(1,26.1) = 5.81, p = .02$. Females overall suppressed μ more than males. This main effect was qualified by two-way interaction with trial type, $F(1,5107.5) = 8.08, p < .01$. Figure 35 depicts the data underlying this interaction, categorically split by gender. We subsequently ran follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$). For some trials, μ suppression decreased linearly as angular disparity increased, $F(1,31.73) = 1485.42, p < .001$, and females suppressed μ more than males, $F(1,26.12) = 7.89, p < .01$. However, in contrast to the electrode analysis, μ suppression decreased equivalently between genders as a function of angular disparity, $F(1,32.25) = 2.28, p > .1$. For different trials, μ suppression also decreased linearly as angular disparity increased, $F(1,1515.08) = 74.41, p < .001$, but μ suppression differences between genders, while significant, were smaller,

$F(1,26.22) = 4.55, p = .04$. Different trial mu suppression did not vary with angular disparity for both genders, $F(1,1593.49) = 0.10, p > .1$.

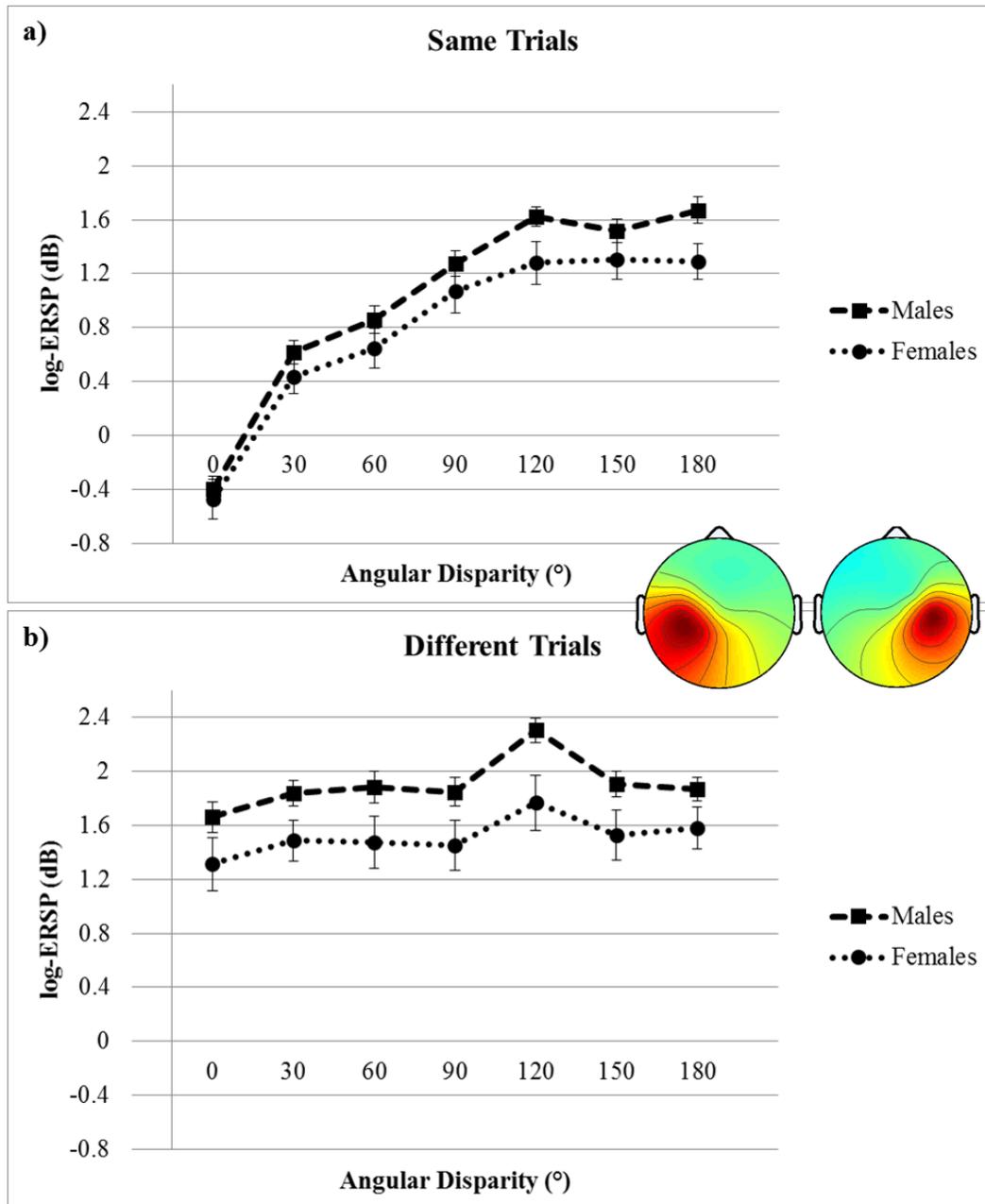


Figure 35. Experiment 3 mean log-ERSP in the MRT collapsed across L & R motor ICs (11 – 13 Hz). Data are averaged within [+300 ms +4300 ms] time window (relative to stimulus onset) as a function of angular disparity and gender for same (a) and different (b) trials. Error bars show standard errors.

We also observed a spatial ability / self-confidence x trial type interaction, $F(1,5106.9) = 6.57, p = .01$. For same trials, high-spatial participants appeared to suppress μ more than low-spatial individuals. However, for different trials, the opposite was true. However, follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) did not yield main effects of spatial ability / self-confidence for either same or different trials (all p 's $> .1$). No other individual difference main effects or interactions emerged.

Fm θ IC. This analysis revealed a three-way interaction between gender / video game experience, angular disparity, and trial type, $F(1,4702.4) = 4.77, p = .03$. As shown in Figure 36, males generally yielded greater $\text{fm}\theta$ power than females for same trials. However, for different trials this difference was only apparent at small angular disparities. We note that follow-up Bonferroni-corrected LMMs within each trial type ($\alpha_{\text{critical}} = 0.025$) did not yield main effects of gender / video game experience nor interactions with angular disparity for either same or different trials (all p 's $> .1$). No other individual difference main effects or interactions emerged.

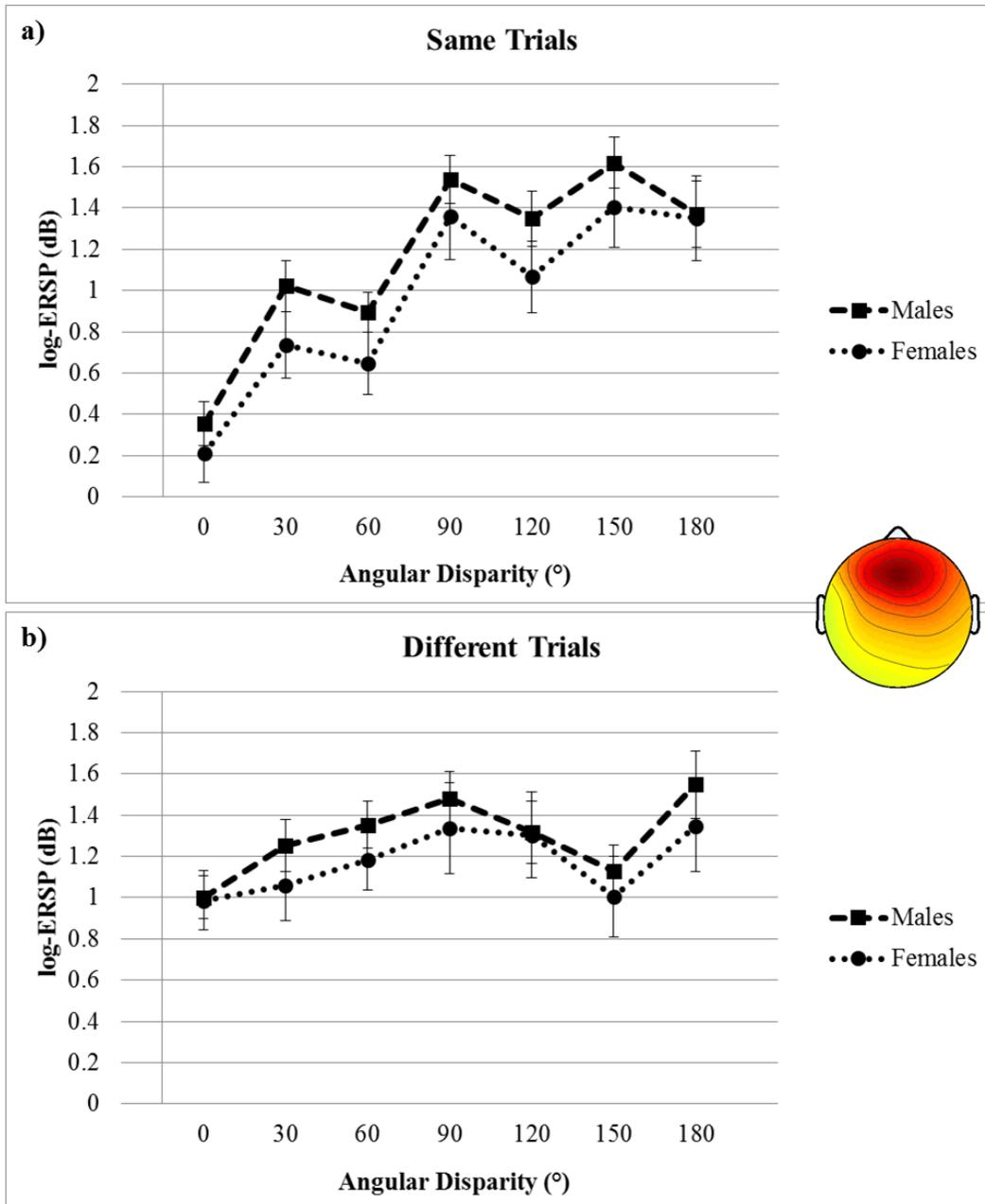


Figure 36. Experiment 3 mean log-ERSP in the MRT for the fmθ IC (5 – 7 Hz). Data are averaged within [+300 ms +4300 ms] time window (relative to stimulus onset) as a function of angular disparity and gender for same (a) and different (b) trials. Error bars show standard errors.

Bilateral Parietal α IC. No individual difference main effects or interaction emerged from the analysis.

Discussion

Experiment 3 provided strong empirical support for the multi-strategy view of mental rotation; mental rotation is covert motor simulation (claim 1) and the MRT recruits both mental rotation and distinct analytic strategies (claim 2). Here we observed and quantified transient event-related spectral perturbations (ERSP) in EEG power, paying special attention to reductions in sensorimotor α -band power (i.e. mu suppression), a well-established neurophysiological correlate of motor simulation and imagery (Pineda, 2005). Under the assumption that strategy use in the MRT is labile, we used mu suppression to infer dynamic use of mental rotation and how it varied due to task difficulty. In addition, using independent component analysis (ICA; Makeig et al., 2004; Onton et al., 2006), we inferred analytic strategy use as well as gained insight into the dynamic engagement of different brain areas in the MRT. Taken together, our findings suggest that a mixture of strategies and processes contribute to MRT performance.

Claim 1: Is Mental Rotation Covert Simulation of Motor Rotation?

Extant evidence of motor cortex involvement in mental rotation is far from definitive, with several experiments observing motor cortical activation in the MRT but others not (Zacks, 2008). Adding to this body of literature, we found evidence for task-related motor cortical activation in the MRT in Experiment 3, consistent with our predictions. Both same and different trials reliably elicited mu suppression, suggesting use of covert motor simulation to complete the task. Initiating about one second post-stimulus onset, we observed sustained mu suppression over bilateral sensorimotor electrodes. While some researchers have

similarly observed mu suppression in hand laterality judgment tasks (HLT; Chen et al., 2013; ter Horst et al., 2013), to our knowledge no other research has demonstrated sensorimotor mu suppression in the classic MRT.

In addition we found that participants elicited more mu suppression for same vs. different trials. We argue that this observation reflects the fact that different trials strongly bias analytic strategies. In their seminal paper introducing the MRT, Shepard & Metzler (1971) did not analyze different trials, arguing that they could not be rotated to achieve congruence. This claim finds some support in the present experiment; different trial error rates remained stable (around 10%) across increasing angular disparities, suggesting a rotation-independent visual comparison strategy. Seminal eye-tracking experiments in the MRT also support this view. Just and Carpenter (1976) analyzed scan paths while participants completed a MRT, focusing their investigation on three theorized stages of task performance: search, transformation and comparison, and confirmation. They found that, for different trials, participants' scan paths contained a large amount (nearly 50%) of confirmation behavior, in which participants scanned back and forth between corresponding parts of the two SM figures. Interestingly, on particularly lengthy responses participants' scan paths suggested visual examination of all possible ways of pairing segments, a strategy that led to a correct "different" response without any transformation at all. This is not to say that mental rotation does not occur for different trials. Rather we argue that it does but to a lesser extent than same trials where it is a more appropriate strategy to use. Said another way, same and different trials possess different *strategy profiles*,

with the former biasing mental rotation and analytic strategies equally and latter preferentially biasing analytic strategies.

Claim 2: Does the MRT Integrate Multiple Strategies?

Experiment 2's physical rotation data suggested that participants use both mental rotation and analytic strategies in the MRT and differentially bias these strategies based on task difficulty. For low difficulty (i.e. small angular disparity) trials, mental rotation is preferred while high difficulty (i.e. large angular disparity) trials bias analytic strategies. Converging evidence from Experiment 3 supported these findings using neurophysiological measures. Consistent with our predictions, we found that as task difficulty (i.e. angular disparity) increased, same trial sensorimotor mu suppression *decreased*. Since mu suppression reliably reflects use of motor simulation, this finding suggests that increasing task difficulty was associated with decreased mental rotation.

In contrast to same trials, different trials elicited distinct patterns of sensorimotor mu suppression as a function of task difficulty. Mu suppression was generally stable across levels of angular disparity but notably reduced at 120°. This finding complements Experiment 1 and 2's findings. When allowed to manually rotate one figure in a different pair, participants' physical rotation converged to similar mean orientations (Exp. 1: 113°, Exp 2: 110°). This suggests that ~120° disparity is a privileged orientation for analytic comparison of different stimuli. Indeed, this orientation may be a *target* orientation to which individuals mentally rotate for different trials, thus explaining the small but significant observed level of mu suppression for different trials. Since 120° is an optimal

view for visual comparison, it follows that no mental rotation and consequently minimal μ suppression occurred for different stimuli at these orientations.

Parietal Contributions to MRT Processing

In addition to motor cortices, posterior parietal cortex (PPC) is frequently implicated in neuroscientific investigations of mental rotation (Zacks, 2008). Researchers have argued that PPC is important for representing spatial maps, action-oriented mental image construction and maintenance, and updating spatial reference frames (Kawamichi, Kikuchi, Noriuchi, et al., 2007; Kawamichi, Kikuchi, & Ueno, 2007; Sack et al., 2008; Sack & Schuhmann, 2012; Sasaoka et al., 2014; Zacks & Michelon, 2005; Zacks, 2008). In the present experiment, we observed sustained parietal α suppression for same and different trials, replicating previous work examining EEG power in the MRT (Gill et al., 1998; Michel et al., 1994; Riečanský & Katina, 2010; Williams et al., 1995). In light of the fact that reductions in α -band power reflect excited cortical networks (Feige et al., 2005; Goldman et al., 2002; Goncalves et al., 2006; Laufs et al., 2003; Laufs et al., 2006; Pfurtscheller et al., 1996), parietal α suppression likely reflects neuronal activation in PPC. As such, we suggest that parietal α suppression magnitude reflects the extent of visuospatial *representational demand* of a cognitive task. This suggestion is in line with previous parametric fMRI results that have demonstrated increases in hemodynamic response and blood flow in PPC associated with increasing task difficulty in the MRT (Carpenter et al., 1999; de Lange, Hagoort, & Toni, 2005; Gogos, Gavrilesco, Davison, Searle, & Adams, 2010). Therefore, the observation that parietal α suppression occurred for both

trial types suggests that, despite their different strategy profiles, parity judgments of same and different trials both depend on visuospatial representation.

We also found that different trials elicited more parietal α suppression than same, though the difference was modest. So far, we have argued that different trials bias analytic strategies which involve visual comparison of key features between stimuli (Bethell-Fox & Shepard, 1988; Geiser et al., 2006; Glück & Fitting, 2003; Just & Carpenter, 1985; Schultz, 1991). In line with this claim, it is not surprising that different trials elicited greater parietal α suppression than same; the analytic strategies that are biased for different judgments likely require increased representational demand relative to same trials which bias mental rotation and analytic strategies equally. Lastly, parietal α suppression varied due to task difficulty. Increasing task difficulty was associated with *increasing* parietal α suppression, suggesting that representational demand increases concomitant with angular disparity. Again, this finding is consistent with the multi-strategy view. If analytic strategy use increases concomitant with increasing task difficulty and the analytic strategy has greater representational demand than mental rotation then it follows that representational demand should increase with increasing task difficulty.

Addressing Electrode Limitations with ICA

The results thus far support both claims of the multi-strategy view; mental rotation is covert motor rotation and the MRT integrates both mental rotation and analytic strategies. But limitations of electrode-based analyses constrain our interpretations. For one, volume conduction is certainly present in our electrode

data. Thus, the sensorimotor mu suppression data inevitably contains parietal α suppression data, and vice versa. This makes it difficult to dissociate contributions of sensorimotor and parietal cortical areas to MRT cognitive processing.

Secondly, we have thus far provided evidence for analytic strategy use indirectly by appealing to difficulty-dependent *decreases* in sensorimotor mu suppression concomitant with *increases* in parietal α suppression. These two neural oscillations reflect use of motor simulation/imagery and visuospatial representation, respectively. However, both mental rotation and analytic strategies depend on representation and evidence for decreasing mental rotation does not necessarily imply increasing analytic strategy use. It would be more convincing to observe oscillations that reflect cognitive processes that likely contribute substantially to analytic visual comparison. To these ends, we used ICA to better separate sensorimotor and parietal contributions to MRT cognitive processing as well as to observe and quantify oscillatory dynamics that reflect working memory processes.

Bilateral Motor IC. We first compared the sensorimotor mu suppression findings between the ICA- and electrode-based analyses. Overall the motor IC data were much less variable, reflecting the ability of ICA to isolate cortical sources and improve signal-to-noise ratio in EEG data. One notable difference was that whereas the electrode analysis yielded overall mu *suppression* the motor IC analysis yielded mu *enhancement*, contrary to our predictions. This peculiar finding may have arisen from our experimental design. Our trial structure included a fixed response window. This served to prevent mu suppression due to

motor preparation of the button response from contaminating the data. However, this fixed response window may have led to proactive response inhibition.

Previous research has demonstrated that primary motor cortex (M1) and surrounding motor areas deactivate with successful stopping in Go/No-go tasks, likely due to inhibitory striatal inputs (Aron & Poldrack, 2006; Vink et al., 2005; Zanbelt & Vink, 2010), and that automatic response inhibition in uncertain contexts leads to inhibitory BOLD response and increased α -band power in the supplementary motor complex (Albares et al., 2014). In line with these studies, the observed increase in motor IC α power may have stemmed from motor inhibition of the button response and was masked at sensorimotor electrode sites by simultaneous volume-conducted parietal α suppression.

An alternate explanation is that mu enhancement somewhat paradoxically arose from motor simulation during mental rotation. The stereotactic coordinates of the motor IC clusters are localized at or near M1. Previous research has demonstrated that the SMA suppresses M1 during motor imagery, suggesting a mechanism by which covert motor simulation prevents overt movements (Kasess, Windischberger, & Cunnington, 2008; Solodkin, Hlustik, Chen, & Small, 2004). Such inhibition may have led to mu enhancement over M1. This possibility cannot be ruled out at this time due to the limited number of electrodes in our montage as well as the low spatial resolution of EEG. However, despite the prevailing mu enhancement of the motor IC data, the central findings from the electrode analysis were supported; mu suppression decreased as a function of task difficulty and differed markedly between same and different trials.

Frontal Midline Theta IC. The most noteworthy contribution of the IC analyses were the observed dynamics of the frontal midline theta (fm θ) IC cluster. So far we have provided direct evidence for mental rotation in the MRT, using sensorimotor mu suppression, but our evidence for analytic strategies remains indirect. The analytic strategy involves visual comparison of key features between figures. This necessarily taxes visual working memory (WM) as the selected segment(s) of one SM figure must be maintained in WM while inspecting the other figure. In addition, particularly for lengthy responses, individuals may consider all possible ways of pairing figure segments, engaging in WM manipulation as well. Previous research has associated positive fluctuations in fm θ power with both WM maintenance and manipulation (Gevins & Smith, 2000; Gevins et al., 1997; Hsieh & Ranganath, 2014; Jensen & Tesche, 2002; Klimesch, 1999; Maurer et al., 2015; Onton et al., 2005; Scheeringa et al., 2009). Thus we used fm θ power as a neurophysiological marker of WM processing and thus analytic strategy use in the MRT.

Consistent with our predictions, we observed overall fm θ power enhancement, suggesting WM maintenance and manipulation processes were engaged in the MRT. Critically, fm θ power increased concomitant with increasing angular disparity for both trial types. Thus the prediction that individuals increasingly bias analytic strategies with increasing task difficulty was supported. To our knowledge this is the first experiment to demonstrate this association between MRT task difficulty and fm θ power and this observation, together with

difficulty-dependent sensorimotor mu suppression decreases, provides strong evidence for the second claim of the multi-strategy view.

Further, different trials elicited greater fm θ power than same. This observation provides additional evidence supporting the claim that different trials bias analytic strategies more than same. The observed trial type x angular disparity interaction reflects this inference as well; different trials yielded greater fm θ power than same at small angular disparities but this difference was not apparent at large angular disparities. This finding suggests that same trials require less WM processing than different when task difficulty is low. However, as difficulty increases, same trials' WM demands "catch up" to different trials.

Parietal α IC. Lastly, we examined the bilateral parietal α IC cluster. This analysis complemented the fm θ analysis as well as yielded both similar and different results from the electrode analysis. As with the motor IC data, parietal α IC data were much less variable than the electrode data. Similar to the electrode results, parietal α IC suppression was observed, was greater for different vs. same trials, and increased linearly with angular disparity. However, we observed a novel trial type x task difficulty interaction. Different trials yielded greater suppression than same at small angular disparities but this difference was not apparent at large angular disparities. This interaction mirrored the fm θ interaction in that it was driven by trial type differences at low angular disparities. Under the assumption that parietal α suppression reflects representational demand, this finding suggests that same trials require less representational processing than different trials at small angular disparities. However, as difficulty increases, same

trials' representational demands “catch up” to different trials. This interaction may have been occluded in the electrode data by prevailing posterior alpha rhythms that are modulated by visual input (Berger, 1929; Hari, Salmelin, Mäkelä, Salenius, & Helle, 1997). Our observation of different findings from the electrode and IC analyses speak to the utility of ICA to attenuate the effects of volume conduction in EEG data (Delorme et al., 2007).

To summarize the IC results, we observed overall sensorimotor mu enhancement, fm θ enhancement, and parietal α suppression, suggesting use of proactive response inhibition, WM processes, and visuospatial representation, respectively. IC cluster power varied as a function of task difficulty. For some trials, concomitant with increasing difficulty, motor and parietal α IC power decreased, suggesting decreased use of mental rotation and increased representational demand, respectively. In contrast, fm θ power increased, suggesting increased WM maintenance and manipulation processes. These difficulty-dependent interactions in spectral power were predicted by the multi-strategy view, which claims that the MRT flexibly integrates both mental rotation and analytic strategies.

The findings also suggested that trial types differ concerning their *strategy profiles*. Some trials equally bias mental rotation and analytic strategies while different trials bias analytic strategies overall. This claim is supported by the observation that different trials elicited less sensorimotor mu suppression, greater parietal α suppression, and greater fm θ power than same trials as well as slower rates of difficulty-dependent changes in the spectral power of these IC clusters.

The results overall paint a picture of a dynamic network of brain regions that is flexibly engaged and whose dynamics are modulated by ongoing changes in task difficulty and trial type. These dynamics in turn reflect real-time changes in the weighting of cognitive processes during MRT parity judgments, including mental rotation, WM, and visuospatial representation. Figure 37 presents a theoretical model of differential weighting of these processes in the MRT as a function of trial type and task difficulty.

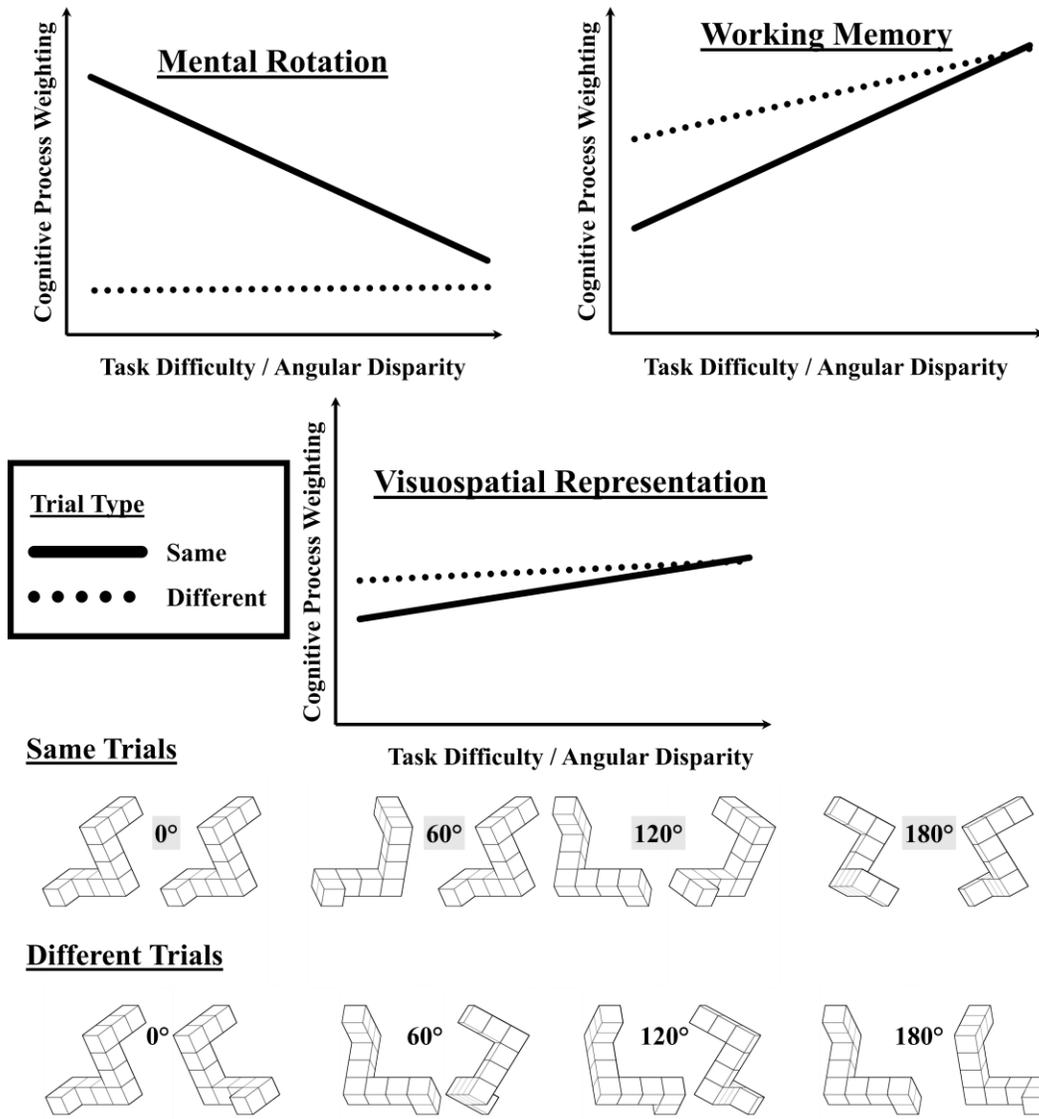


Figure 37. Theoretical model of differential weighting of cognitive processes in the MRT as a function of trial type and task difficulty. Weights were informed by IC analysis results.

Individual Differences

This dynamic network was in turn modulated by individual differences. At the outset we predicted that high spatial ability participants would more flexibly (and optimally) trade off between strategies relative to low, consistent with

Experiment 2's findings. This flexibility would be reflected by a steeper decline in sensorimotor mu suppression and a steeper incline in $fm\theta$ enhancement concomitant with increasing angular disparity. We also predicted that females would elicit more mu suppression than males, consistent with previous research (Cheng et al., 2008), and less $fm\theta$ enhancement than males. This finding would suggest that gender effects in MRT performance stem from females' preference to mentally rotate, even when such strategies are not optimal (Hegarty, 2010).

Analysis of the motor IC cluster yielded some evidence that spatial ability was associated with optimal strategy use; high-spatial participants elicited greater motor IC suppression for same trials and less suppression for different trials, relative to low-spatial participants. However, the critical three-way interaction was not significant and we did not observe spatial ability effects on $fm\theta$. Recall that Experiment 2's PRT_{NVF} data suggested that high-spatial participants more optimally traded off between strategies for same trials in changing difficulty contexts. The present neurophysiological data did not support this conclusion. One possible explanation for these conflicting findings is that spatial ability is associated with dual-task performance in the PRT_{NVF} , rather than strategy use. More research is needed to clarify the links between physical rotation and cognitive strategies in the MRT.

However, we did observe influences of gender in the present experiment. Sensorimotor mu suppression was greater for females than males for both trial types, consistent with our predictions. Interestingly, while same trial mu suppression decreased as function of angular disparity for both genders, it

decreased more slowly for females than males. This finding suggests that females biased mental rotation more than males and persisted even for high difficulty trials, in which analytic strategies are more optimal. Such biasing of mental rotation may disadvantage females in the MRT, especially in high task difficulty contexts. However, it is important to note, that while the gender main effect was also observed in the motor IC cluster, the interaction with angular disparity was not. This difference between analyses may have been driven by volume conduction of parietal α suppression, which also differed between genders. Thus it remains unclear whether the difference in μ suppression between genders observed here reflects different MRT strategy profiles or broader physiological differences (Cheng et al., 2008). It should also be noted that the present gender effects opposed those found in Experiment 2, where the PRT_{NVF} data suggested males preferentially used mental rotation. As mentioned above, more research is needed to clarify the extent to which the PRT_{NVF} reflects cognitive strategies and dual task interference. EEG data collection during the PRT_{NVF} may be particularly helpful in this regard.

Lastly, in the present analyses gender was linked with video game experience in a composite factor score due to their inter-correlation. Thus observed gender effects may reflect differential video game experience. In light of this observation and others (Feng et al., 2007), future research on the MRT and other spatial tasks should consider and/or manipulate video game experience in their designs in order to disentangle independent contributions of these factors.

Additional Considerations and Limitations

Overall, the results from both the electrode and ICA analyses support the multi-strategy view; mental rotation is covert motor rotation and the MRT integrates both mental rotation and analytic strategies. Results from the two analyses generally converged on the same conclusions but in some cases differed. We argue that the ICA analyses' divergent observations are important and speak to the utility of ICA decomposition for attenuating volume conduction effects in scalp EEG. Such decomposition may be a required step to observe subtle and temporally dynamic interactions between cortical sources in the MRT network. The ICA results also emphasize the difficulty of inferring motor simulation in the MRT; both motor preparation and inhibition of the button response may contaminate ongoing mental rotation-related motor activity. Thus, future work should carefully consider how behavioral responses impact neuroscientific measures of motor activation. Perhaps voice response, as employed in Experiments 1 and 2, may attenuate behavioral response motor contamination, or perhaps, behavioral responses should be eschewed entirely.

Along similar lines, one could argue that the observed difficulty-dependent decrease in mu suppression for some trials merely reflects trading off between initial enhancement of motor IC power due to proactive response inhibition and later suppression due to response preparation. The argument goes thusly. Parity judgments of difficult trials take longer than easy trials and consequently proactive response inhibition should also take longer. At the decision point ("the figures are the same"), processing switches from inhibiting

the behavioral response (mu enhancement) to preparing it (mu suppression). If this decision point is temporally shifted later as a function of task difficulty then difficult trials would be disproportionately made up of response inhibition vs. response preparation processing, leading to less mu suppression overall. In contrast, easy trials' decision points would occur sooner, and thus processing would be biased towards motor preparation, leading to greater mu suppression. However, closer examination of the temporal dynamics of motor IC power do not support this account. Deflection from peak enhancement to suppression commenced at similar times across levels of angular disparity, ranging from ~800 ms post-stimulus onset for 0° disparity and ~1600 ms for 180°. Further, deflection points for each difficulty level were not temporally ordered and, outside of the two lowest difficulty levels (0° & 30°), they all occurred within 200 ms of each other. Thus it is unlikely that differential mu suppression across levels of task difficulty was due to temporal shifting of a motor response inhibition and preparation trade-off point.

Another limitation concerns the spatial resolution of EEG. Even with the aforementioned advantages of ICA, our findings do not possess the spatial resolution to make conclusions about activations of specific cortical regions. Thus when we conclude that motor activation decreases with increasing task difficulty, we cannot localize that activity to specific motor regions. Further, we included only a subset ($n = 19$) of electrodes from our 32-channel array for our electrode- and ICA-based analyses. As dipole source localization error is influenced by the number of recording sites (Murro, Smith, King, & Park, 1995), this decision

certainly increased the localization error of our IC dipoles. While this is problematic it is not damning to our conclusions as we only used dipole localization to aid in clustering spatially distinct, non-overlapping ICs, and not to precisely localize their cortical sources.

A broader criticism of the present experiment takes aim at our assumptions concerning links between IC components and cognitive processes. While the functional significance of and cognitive processes underlying motor ICs are well-established (Makeig et al., 2002; Pineda, 2005), the μ and parietal α components are less so. We have argued that μ reflects WM processing. Yet, oscillatory changes in μ power have been linked to a variety of higher-order cognitive processes, including cognitive control and sustained attention (Cavanagh & Frank, 2014; Hanslmayr et al., 2008; Sauseng et al., 2007) as well as general fatigue and cognitive load (Antonenko, Paas, Grabner, & van Gog, 2010; Wascher et al., 2014). Thus, the observed difficulty-dependent increases in μ power in the MRT may reflect increases in sustained attention or merely be epiphenomenal of increased task difficulty.

Similarly, we have argued that parietal α suppression reflects representational demand but previous research has linked it to WM processing and cognitive load (Klimesch, 1999; Klimesch, Schimke, & Pfurtscheller, 1993; Gevins et al., 1997). Yet, other studies have found parietal α *enhancement* in memory tasks (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999; Krause, Lang, Laine, Kuusisto, & Pörn, 1996; Jensen, Gelfand, Kounios, & Lisman, 2002; Sauseng et al., 2009; Shack & Klimesch, 2002). Differential

visuospatial representational demands may explain these conflicting findings. Parietal α suppression likely occurs during difficult WM tasks, such as the *n*-back, that recruit visualization strategies reliant on visuospatial representations. In less demanding memory tasks, such as the Sternberg task, visuospatial strategies are less necessary and are likely inhibited to prevent distraction, leading to parietal α enhancement (Jensen et al., 2002; Hsieh, Ekstrom, & Ranganath, 2011). Thus, while oscillatory dynamics of parietal α certainly play a role in WM processing, they may depend on the extent to which visuospatial representation is useful for optimal task performance. As discussed previously, the MRT is a demanding task that engages several strategies, all of which depend, in part, on visuospatial representation. As such, we maintain that observed parietal α suppression in the present experiment likely reflects the use of visuospatial representation and not WM maintenance.

Lastly, we have thus far framed the present findings as supporting a trade-off between mental rotation, the covert simulation of motor rotation, and analytic strategies that rely on visual comparison. However, an alternative explanation may account for the observed flexible weighting of cognitive processes in the MRT; individuals may have primarily switched between mental rotation sub-strategies. Extant meta-analyses of the mental rotation literature suggest that effector- and object-based mental rotation strategies are flexibly applied across studies due to several experimental factors (Tomasino & Gremese, 2015; Zacks, 2008). Effector-based rotation involves mentally simulation manual rotation, a strategy that likely recruits motor cortical areas, while object-based rotation

involves simulating externally-guided rotation, a strategy that may engage motor cortical areas less or not at all (Zacks, 2008). If participants increasingly unconsciously adopt object-based mental rotation at the expense of effector-based as task difficulty increases, decreases in motor cortical activation would be expected. This account seems unlikely, however, given that both sub-strategies have been shown to elicit premotor activation, suggesting that at least some motor simulation occurs in both cases (Kosslyn et al., 2001). However, the possibility cannot be ruled out by the present experiment's design which does not possess the spatial resolution necessary to distinguish contributions of distinct motor cortical areas.

Conclusions

In sum, Experiment 3 provided strong corroborating evidence for the multi-strategy view of mental rotation and upheld the main conclusions of Experiment 2. Cognitive processing in the MRT involves mental rotation, covert motor simulation that elicits sensorimotor mu suppression, and MRT performance relies on flexible trade-offs between mental rotation and analytic strategies. Our ICA-based analyses, in particular, provided insight into the dynamics of cortical activation subserving this strategy flexibility. We found that, for some trials, low levels of task difficulty bias cognitive processing towards mental rotation and away from WM and visuospatial representation processes, though both certainly play a role. In contrast, when task difficulty is high, mental rotation is de-emphasized and WM and visuospatial demands increase, reflecting preferential use of analytic strategies that involve visual comparison of key object features.

We argue that this ability to flexibly and automatically choose between mental simulation and more analytic forms of thinking is a domain-general cognitive principle that underlies aptitude and spatial intelligence in a variety of cognitive domains (Geiser et al., 2006; Hegarty, 2010; Taylor & Brunyé, 2013).

GENERAL DISCUSSION

The present series of experiments investigated the cognitive processes underlying mental rotation and the cognitive strategies flexibly used in the mental rotation task (MRT). In doing so, we advanced and experimentally evaluated *the multi-strategy view of mental rotation*. According to this view, mental rotation is covert simulation of motor rotation, a cognitive process that depends, in part, on neural computations in motor cortical areas that subserve motor planning and anticipation (Wexler et al., 1999). Further the MRT does not solely engage this process but rather dynamically integrates both mental rotation and analytic strategies. Experiment 1 used a novel physical rotation paradigm in which participants physically rotated figures to aid their parity judgments. We found behavioral similarities between mental and physical rotation, suggesting similar underlying cognitive processes. In addition, our findings cast doubt on a central assumption in the mental rotation literature, namely that mental rotation involves rotation of analogous mental percepts to matching orientations.

Spurred by this discovery, Experiment 2 replicated and expanded these findings. Here, we analyzed physical rotation behavior that mirrored covert mental rotation processes. Strikingly, we found that, in some cases, rotation resembled that observed in Experiment 1, suggesting mental rotation. Yet, in

other cases rotation was minimal, suggesting analytic strategies that rely on visual comparisons of key features. Importantly, task difficulty (i.e. angular disparity) strongly influenced strategy bias; easy trials biased mental rotation while difficult trials biased analytic strategies.

Experiment 3 further investigated this potential trade-off between MRT strategies using time-frequency analyses of EEG. We found that as difficulty increased, sensorimotor mu suppression, a neurophysiological marker of motor simulation and imagery, decreased. Simultaneously, frontal midline theta enhancement and parietal alpha suppression increased, which reflect increased WM use and visuospatial representation processes, respectively. Thus, Experiment 3 provided converging evidence that individuals trade off between mental rotation and analytic cognitive strategies in the MRT based on task difficulty. We suggest that this ability to flexibly and automatically choose between mental simulation and more analytic forms of thinking is a key component of spatial intelligence. Taken together, findings from the present series of experiments suggest that there is more to the MRT than mental rotation. Rather than solely engaging mental rotation, the MRT dynamically integrates both mental rotation and analytic strategies.

Implications

The present findings have implications for continuing spatial cognition research as well as real-world applications. First, our finding that task difficulty reliably influences strategy use in the MRT is significant given that researchers have historically considered the positive linear relationship between RT and

angular disparity as behavioral evidence of mental rotation. Our findings suggest reevaluation of this generally accepted dogma and point to the necessity for future research to consider how task difficulty as well as other factors may influence strategy use in the MRT and other spatial tasks. MRT-based research has also tended to omit investigation of “different” trials, another misstep in our view. As the present experiments show, scrutinizing different trials can yield fresh insights, especially regarding analytic strategies.

Overall, we argue that the consistently replicated angular disparity effect does not purely reflect mental rotation but rather represents the tip of the iceberg of underlying cognitive strategies. The novel behavioral and neural methods presented herein offer a means to investigate the strategies that lie below the surface. More broadly, we encourage researchers, across the subdomains of cognitive science, to apply strategy-shift models to their research questions (Botella et al., 2009; Glück & Fitting, 2003; Kyllonen et al., 1984; Lohman, 1988). Doing so may shed light on yet-unsettled debates in mental rotation and other domains.

For example, consider gender differences, which are often observed in the MRT but also much debated. If the MRT integrates different strategies then gender differences may stem from different strategy profiles rather than differences in mental rotation ability (Butler et al., 2006; Bryden, 1980; diSessa, 2004; Glück & Fitting, 2003; Voyer & Saunders, 2004). For example, males and females perform equivalently in tasks that recruit mental rotation (Alexander & Evardone, 2008; Christova et al., 2008) and gender differences in the MRT appear

to emerge around 7 to 8 years of age, about the same time that analytic strategies come online (Frick, Daum, Walser, & Mast, 2005; Frick et al., 2014; Neuburger, Jansen, Heil, & Quaiser-Pohl, 2011; Titze, Jansen, & Heil, 2010). In our present investigations, we found that females elicited greater μ suppression than males, consistent with previous work (Cheng et al., 2008). These findings suggest that females bias mental rotation more than males and that the “male advantage” in the MRT may stem from males’ stronger disposition to use alternative analytic strategies when such strategies seem optimal in the current context. In other words, males may have better meta-representational competence (diSessa, 2004; Hegarty, 2010), knowing when to use non-rotational analytic strategies, but are not better at mental rotation per se. This inference is powerful because it offers a path to intervention. For example, targeting instructions to emphasize analytic strategies may reduce gender differences in spatial cognition (Stieff, 2007).

Similar strategy-based instructional targeting can be applied to education. Increasing research has linked spatial task performance with success in science, technology, engineering, and mathematics (STEM: Uttal, Miller, & Newcombe, 2013). This research suggests that spatial ability is associated with STEM aptitude and that spatial training may improve STEM learning (Bruce & Hawes, 2014; Y. Cheng & Mix, 2014; Newcombe & Frick, 2010; Uttal et al., 2013). Yet, spatial training is all but missing in elementary education (National Research Council, 2006). Instructional manipulatives may offer a ready means to integrate spatial training into education and target children’s preferred cognitive strategies.

Manipulatives are concrete physical objects used to teach abstract concepts via hands on learning (Boggan, Harper, & Whitmire, 2010; Carbonneau, Marley, & Selig, 2013; Uttal, O’Doherty, Newland, Hand, & DeLoache, 2009). If children are predisposed to use mental rotation (Frick et al., 2014) then early STEM education may benefit from using manipulatives because they present information in a readily-accessible format (Pouw, Van Gog, & Paas, 2014). Indeed, in the domain of mathematics, manipulatives have been shown to improve problem solving for topics that are easy to represent spatially such as fractions and the number line (Carbonneau et al., 2013; Gunderson, Ramirez, Beilock, & Levine, 2012). Further, gesture, both by instructors and students, improves math understanding (Cook, Duffy, & Fenn, 2013; Goldin-Meadow, Cook, & Mitchell, 2009; Novack, Congdon, Hemani-Lopez, & Goldin-Meadow, 2014). The newly adopted Common Core mathematics standards in the United States emphasize constructivism or learning through self-discovery (Germain-McCarthy & Gill, 2014). Given this new pedagogical landscape, using manipulatives, gesture, and other techniques that cater to children’s cognitive strategies may aid in math and science conceptual understanding.

Future Directions

The present findings provide several insights for future research. First, the converging findings from Experiment 2 and 3 speak to the robustness of dynamic strategy use in the MRT, but also to the heretofore undiscovered utility of continuous measures of physical rotation behavior. Considering these measures are relatively straightforward and inexpensive to collect relative to neuroimaging,

we believe that they are a promising new tool to investigate cognitive strategies in a wide variety of tasks. For example, automated tracking and recognition of manual gestures may permit inference of underlying cognitive strategies during spatial problem solving (Parvini & Shahabi, 2006; Srilatha & Saranya, 2014).

We also stress the need for continued work examining electrophysiological markers of cognitive strategy use. Experiment 3 demonstrated the utility of EEG time-frequency analysis for detecting covert use of mental rotation and analytic strategies in the MRT. Future research should continue to investigate strategy use in other cognitive tasks using EEG as has been done in recent work on hand laterality judgment tasks (Chen et al., 2013; ter Horst et al., 2013). This approach may be particularly influential in studies of mental rotation development. EEG can be collected from infants and children more easily than neuroimaging and previous research has shown that 18 - 30-month old infants both elicit mu suppression during action execution and observation (Marshall, Young, & Meltzoff, 2011; Nyström, Ljunghammar, Rosander, & Von Hofsten, 2011; Warreyn et al., 2013) and frontal midline theta enhancement during memory- and attention-demanding tasks (Cuevas, Raj, & Bell, 2012; Orekhova, Stroganova, & Posikera, 1999). Future work could examine the developmental trajectory of cognitive strategies using time-frequency analysis of EEG. In addition, EEG allows for greater levels of physical movement than neuroimaging. This could permit study of simultaneous gesture or movement and its influence on cognitive strategies (Quandt, Marshall, Shipley, Beilock, & Goldin-Meadow, 2012).

Another potential application for mu suppression is in brain-computer interfaces (BCIs), which use brain activity as an input for devices and software. Previous research has demonstrated the utility of mu suppression in BCIs; individuals can voluntarily control a cursor with mu suppression alone (Wolpaw & McFarland, 2004) and mu suppression can predict voluntary movement before it occurs (Bai et al., 2011). Increasingly, BCI researchers have considered brain activity as a secondary rather than primary source of information for interfaces (Cutrell & Tan, 2008; Zander, Kothe, Jatzev, & Gaertner, 2010). Such passive BCIs could detect mu suppression during cognitive tasks using machine learning classification and then reactively modify task parameters in real-time. This technology could be applied to cognitive training. For example, training with *neurofeedback*-based BCIs has been shown to increase mu suppression in motor imagery tasks (Kaiser et al., 2014; Zich, De Vos, Kranczioch, & Debener, 2015). Along similar lines, a mu suppression-based BCI could detect and reward participants when they mentally rotate (and elicit mu suppression) as a means to train mental rotation ability (Hanslmayr, Sauseng, Doppelmayr, Schabus, & Klimesch, 2005; Zoefel, Huster, & Herrmann, 2011). Similar methodologies could be applied to other oscillations that are associated with MRT performance, such as frontal midline theta or parietal alpha.

Neurostimulation of ongoing neuronal oscillations is another exciting potential means of optimizing cognitive strategy use in the MRT and other spatial tasks. In particular, transcranial alternating current stimulation (tACS) can deliver electrical oscillatory (sine-wave) currents to cortical sites within operator-

specified frequency ranges. These currents are believed to entrain with or synchronize neuronal networks, leading to changes in ongoing neuronal oscillations (Antal & Paulus, 2013; Herrmann, Rach, Neuling, & Strüber, 2013; Horschig, Zumer, & Bahramisharif, 2014; but see: Brignani, Ruzzoli, Mauri, & Miniussi, 2013). Computer simulations and *in vivo* recordings suggest that tACS increases oscillatory synchronization in a frequency-specific manner (Ali, Sellers, & Fröhlich, 2013; Merlet et al., 2013). For example, applying 10 to 20 minutes of tACS at individual EEG alpha frequency (IAF) results in enhancement of EEG alpha amplitude in the range of the IAF (Zaehle, Rach, & Herrmann, 2010), an effect that can last for up to 30 minutes post-stimulation (Neuling, Rach, & Herrmann, 2013). Such stimulation can yield behavioral effects, including eliciting perceptual sensations, influencing motor responses, and modifying task performance (Herrmann, Strüber, Helfrich, & Engel, 2015). Importantly, recent work has demonstrated that tACS can influence ongoing sensorimotor mu rhythms (Feurra, Paulus, Walsh, & Kanai, 2011; Feurra et al., 2013; Gundlach, Sehm, Müller, & Villringer, 2012; Wach et al., 2013). Future research could apply IAF-band tACS to sensorimotor sites to increase mu rhythm amplitudes in the MRT. Since mu suppression reflects motor imagery use, such tACS-induced mu enhancement may facilitate analytic strategy use by deemphasizing mental rotation. Similarly, theta band tACS applied to frontal cortical sites has been shown to improve working memory capacity and matching performance (Meiron & Lavidor, 2014; Polanía, Nitsche, Korman, Batsikadze, & Paulus, 2012), likely by increasing frontal midline theta power. Together, simultaneous sensorimotor

mu and frontal midline theta enhancement, induced by tACS, could modify strategy use in the MRT and other spatial tasks. Moreover, tACS could be dynamically applied based on task difficulty, promoting cognitive enhancement only when it is need and/or desirable.

Lastly, Experiment 3 also demonstrated the utility of decomposing EEG using independent component analysis (ICA). Analyses of independent component activations yielded novel conclusions that were not present in the raw EEG data, likely due to volume-conduction of central and parietal sources. In addition, ICA, combined with dipole localization, estimates the spatial locations of cortical source patches, an important feature when scrutinizing motor cortex activity, and research to improve estimation accuracy is ongoing. For example, recent research has demonstrated greatly reduced dipole localization error using high density electrode sets coupled with computational estimation of brain-to-skull conductivity (Acar, Acar, & Makeig, 2016). Such methods, in combination with MR imaging-derived electrical head models may bring EEG spatial resolution to the sub cm² scale, allowing it to localize distinct motor cortical sources.

Concluding Remarks

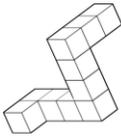
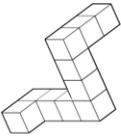
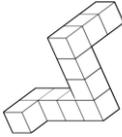
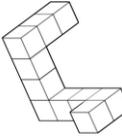
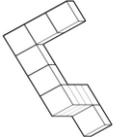
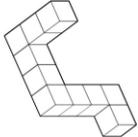
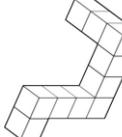
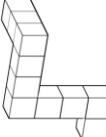
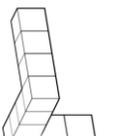
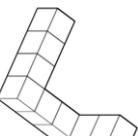
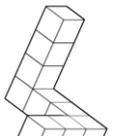
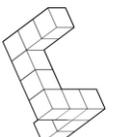
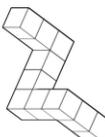
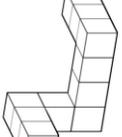
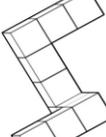
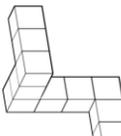
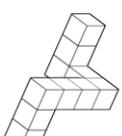
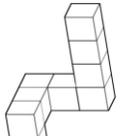
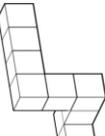
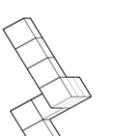
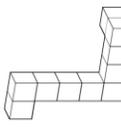
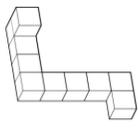
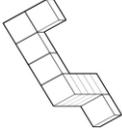
In a series of three experiments, we advanced and experimentally evaluated the *multi-strategy view of mental rotation*, which posits that mental rotation is covert simulation of motor rotation and that the MRT does not solely engage this process but rather integrates both mental rotation and analytic strategies. The present findings supported both claims of this view using

innovative behavioral and neuroscientific methodologies. The multi-strategy view provides a powerful reconceptualization of the existing mental rotation literature and helps explain why numerous experimental design factors influence the observation of motor simulation in the MRT. From a theoretical perspective, future research using the MRT and other spatial tasks should consider *strategy profiles* of their participant samples and experimental designs and should frame findings not as differences in mental rotation ability but as differences in strategy bias. From a methodological perspective, future research should use continuous measures of physical rotation behavior as well as electroencephalographic markers of motor simulation to classify cognitive strategies in real-time. This approach may have particular promise for revealing the developmental trajectory of mental rotation in infants and children. Lastly, continued work is needed to clarify the links between mental rotation ability and STEM success as well as to examine the impact of pedagogical interventions that target children's preferred cognitive strategies, such as instructional manipulatives. Doing so can have broad impact across the disciplines of cognitive science and education.

In closing, mental rotation is a fascinating cognitive process whose significance and widespread recognition is well-deserved. We hope that future research in this area considers the issues raised in this dissertation as mental rotation research continues to fuel discovery in cognitive science.

APPENDIX A

Example Shepard and Metzler (1971) MRT trials. Figure images taken from Peters and Battista's (2008) stimulus library.

Angular Disparity	Same (Identical)		Different (Mirrored)	
0°				
30°				
60°				
90°				
120°				
150°				
180°				

APPENDIX B

Angular-disparity calculation

$$\text{Quaternion}_{\text{Target}} (Q_T) = [x_1 \ y_1 \ z_1 \ w_1]$$

$$\text{Quaternion}_{\text{Response}} (Q_W) = [x_2 \ y_2 \ z_2 \ w_2]$$

$$[x_3 \ y_3 \ z_3 \ w_3] = Q_T \times Q_W^{-1}$$

$$\text{Angular Disparity (AD)} = 2 \times \left(\frac{180 \times \cos^{-1} w_3}{\pi} \right)$$

Angular-disparity transformation

If $AD > 180$ then $AD = (360 - AD)$

else

$AD = AD$

APPENDIX C

MATLAB packages used for data mining in Experiment 2

Dynamic Time Warping

Author: Quan Wang

URL: <http://www.mathworks.com/matlabcentral/fileexchange/43156-dynamic-time-warping--dtw->

K-medoids cluster analysis

Author: Benjamin Sapp

URL: <http://www.mathworks.com/matlabcentral/fileexchange/28860-kmedoids>

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