

## Visuomotor mental rotation: the reaction time advantage for anti-pointing is not influenced by perceptual experience with the cardinal axes

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**Abstract** In the visuomotor mental rotation (VMR) paradigm, participants execute a center-out reaching movement to a location that deviates from a visual cue by a predetermined instruction angle. Previous work has demonstrated a linear increase in reaction time (RT) as a function of the amplitude of the instruction angle (Georgopoulos and Massey in *Exp Brain Res* 65:361–370, 1987). In contrast, we recently reported a RT advantage for an instruction angle of 180° relative to a 90° angle (Neely and Heath in *Neurosci Lett* 463:194–198, 2009). It is possible, however, that perceptual expertise with the cardinal axes, which are perceptually familiar reference frames, influenced the results of our previous investigation. To address this issue, we employed a VMR paradigm identical to that of our previous work, with the exception that the stimulus array was shifted 45° from the horizontal and vertical meridians. Our results demonstrated that RTs were fastest and least variable when the instruction angle was 0°, followed by 180°, which in turn, was faster than 90°. Such findings establish that the RT advantage for the 180° instruction angle is not influenced by perceptual expertise with the cardinal axes. Moreover, the present results provide convergent evidence that RT is not determined by the angle of rotation; instead, they indicate that response latencies reflect computational differences in the complexity of response remapping.

**Keywords** Sensorimotor transformations · Reaction time · Visuomotor mental rotation · Vector inversion · Reaching

### Introduction

The phenomenon of mental rotation, the imagined manipulation of a two- or three-dimensional object, was first characterized by Shepard and colleagues in a series of experiments in which observers were simultaneously presented with two visual objects at different orientations (e.g., Cooper and Shepard 1973; Shepard and Cooper 1982; Shepard and Metzler 1971). Observers were asked to report whether the objects were identical to one another. The cardinal finding of this work was the demonstration that the time required to make a decision [reaction time (RT)] increased linearly with the angular disparity between the objects. Of greater interest to the motor control literature, however, is the visuomotor mental rotation (VMR) task—a variant of the mental rotation task (Georgopoulos and Massey 1987). In the VMR paradigm, participants complete a center-out reaching movement to a location that deviates from a visual cue by a predetermined instruction angle. For example, if given a 90° clockwise (CW) instruction angle and a visual stimulus at the 3'o'clock position, the correct response requires pointing to the 6'o'clock position. In accord with the mental rotation literature, Georgopoulos and Massey report a monotonic increase in RT as a function of increasing angle for angles of 5°, 10°, 15°, 35°, 70°, 105° and 140°. These findings led Georgopoulos and Massey to posit that the VMR task is mediated via the mental rotation of an imagined movement vector. Specifically, the *mental rotation model* asserts that the vector between the stimulus and initial limb position is calculated, then mentally rotated

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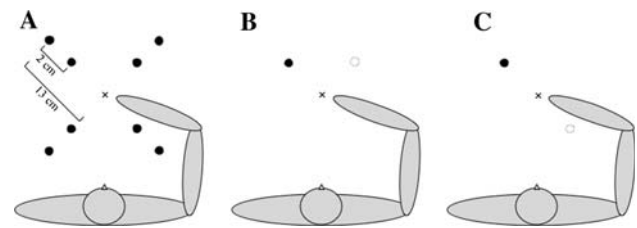
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until it reaches the appropriate direction, at which point it is translated into motor output (Georgopoulos and Massey 1987). Moreover, single cell recordings in non-human primates has shown that directional specific neural population vectors initially reflect the direction of the visual stimulus and then shift gradually to the direction of the motor response (Georgopoulos et al. 1989; Lurito et al. 1991). Such results were interpreted as evidence for the *mental rotation model* (see Figure 1 of Georgopoulos et al. 1989).

In contrast to the *mental rotation model*, we recently provided behavioral evidence that 90° and 180° VMR are not similarly mediated by a temporally monotonic mental rotation strategy (Neely and Heath 2009). In our study, participants completed center-out pointing movements in four tasks: a pro-pointing task (PRO) in which they pointed directly to the target stimulus; an anti-pointing task (ANTI) in which they pointed to a location 180° from the target stimulus; a CW and a counterclockwise (CCW) rotation task in which they pointed to a location 90° CW or CCW to the target stimulus. Importantly, target stimuli were presented along the vertical (Experiment 1) and horizontal (Experiment 2) meridians. We found that RTs for the PRO task were faster and less variable than those for the ANTI task, which in turn elicited faster and less variable RTs relative to the CW and CCW tasks. Based on these findings, we proposed that the cognitive demands of response preparation for the ANTI task were reduced in comparison to CW and CCW tasks because the requisite sensorimotor transformations were completed within the same movement plane as the target stimulus. In contrast, the CW and CCW tasks required a more complex transformation of response parameters in a direction orthogonal to the original stimulus-driven response.

One possible limitation of our previous work (Neely and Heath 2009) was that visual stimuli were presented along the cardinal axes—perceptually familiar egocentric reference frames. Thus, our findings may have been influenced by an enhanced ability to derive the egocentric location of the target stimulus or movement endpoint in the ANTI task. Specifically, response planning may have been computationally less demanding for the ANTI task because both target stimulus and ultimate movement endpoint were congruent with the vertical (Experiment 1, Neely and Heath 2009) or horizontal (Experiment 2, Neely and Heath 2009) meridian. Indeed, Purves and colleagues have demonstrated that past perceptual experience influences visual processing; more importantly, they have shown that as a result of this experience, straight lines and right angles are perceived with minimal distortion in comparison to other orientations and angles (Howe et al. 2006; Nundy et al. 2000). Further, Heath and colleagues have shown that the ANTI task is cognitively driven and is mediated by visuoperceptual networks (Heath et al. 2009a, b). Thus, due to the cognitive



**Fig. 1** **a** Birds eye view of the stimulus configuration. Target stimuli were presented at two eccentricities in the *upper left*, *upper right*, *lower left* and *lower right* visual quadrants. **b** In the CW task, the correct motor response (represented by a *hatched circle*) to a target stimulus appearing in the *upper left* quadrant is in the *upper right* visual field. **c** In the ANTI task, the correct motor response to a target stimulus appearing in the *upper left* quadrant is in the *lower right* visual field

nature of VMR tasks, it is possible that our previous pattern of results was a consequence of perceptual expertise with the cardinal axes. The present work therefore sought to determine if response latencies in the ANTI, CW and CCW tasks are influenced by perceptual familiarity with the cardinal axes. To that end, we employed a VMR paradigm identical to that of our previous work (Neely and Heath 2009), with the exception that the stimulus array was shifted 45° (see Fig. 1). This paradigm provided a framework to determine whether the ANTI, CW and CCW tasks are similarly mediated via the mental rotation of an imagined movement vector when target stimuli and motor output occur in perceptually less familiar regions of the visual field. If the present study replicates our previous pattern of results, then there exists convergent evidence to assert that the response latencies in ANTI, CW and CCW tasks are not determined by the angle of rotation (i.e., as stated in the *mental rotation model*), but rather reflect computational differences in the complexity of response remapping.

## Methods

### Participants

Fifteen university students (7 male; 20–31 years of age) volunteered to participate in this study. All participants were naïve to the hypothesis being tested, were self-identified as right-hand dominant, and had normal or corrected-to-normal vision. All work was conducted in accordance with the Declaration of Helsinki (1964) and the guidelines established by the Office of Research Ethics, University of Western Ontario.

### Apparatus and stimuli

Participants completed goal-directed reaching movements while seated at a virtual aiming apparatus (for a schematic of the apparatus see Neely et al. 2008). Visual stimuli were

projected from an inverted computer monitor (DELL: 1707FP, 8 ms response rate; Austin, TX, USA) placed on the top shelf of the apparatus to a half-silvered mirror that comprised the middle shelf of the apparatus. Participants completed pointing movements to virtual targets on the bottom shelf of the apparatus (i.e., the reaching surface). The distance between the monitor and the mirror, and the mirror and the pointing surface was 34 cm, thus, the optical geometry was such that stimuli projected on the mirror were perceived as being located on the pointing surface. The room lights in the experimental suite were extinguished for the duration of the testing session. Extinction of the room lights, in combination with the half-silvered mirror, prevented participants from directly viewing their limb. Eye movements were monitored via a 120 Hz video-based eye-tracking system (Applied Science Laboratories: H6 HS CN; Bedford, MA, USA). Participants' midline was centered on the viewing area and this position was maintained via a chinrest. All experimental events were controlled via MATLAB (7.6: The MathWorks; Natick, MA, USA) and Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997).

Visual stimuli included a white fixation cross (10 mm × 10 mm) and eight white target stimuli (10 mm diameter circles) all of which were presented against a high-contrast black background. Target stimuli were projected 45° from the horizontal and vertical meridians, in the upper left, upper right, lower left and lower right visual fields (see Fig. 1). Further, target stimuli were located at two eccentricities, 11 and 13 cm from the home position, and are henceforth referred to as near and far targets, respectively. The location of the fixation cross was consistent with the starting position of the limb and was marked by a tactile cue (i.e., a small switch). As a result, participants were able to compute an appropriate internal representation of limb position in advance of each pointing response (Prablanc et al. 1979).

## Procedure

At the start of each trial, participants directed their gaze and placed their right index finger (i.e., the reaching limb) on the visual fixation cross. After 1,000 ms, a target stimulus appeared in one of eight locations for 50 ms. Onset of the target stimulus served as the movement initiation cue. Importantly, because the oculomotor system may influence an ensuing manual response (Bock 1986; van Donkelaar 1997), the fixation cross was displayed for the duration of the trial and participants were directed to maintain fixation until completion of their response.

Participants completed center-out pointing movements from a central start position in four tasks: PRO, ANTI, CW and CCW (see Fig. 1). Tasks were completed in separate

and randomly ordered blocks of trials; therefore participants had advance knowledge of the angle of rotation required in an upcoming trial. Ten trials were completed for each visual stimulus location and eccentricity combination. The presentation of stimulus location and stimulus eccentricity was randomized within each block of trials. In total, participants completed 320 trials in an experimental session.

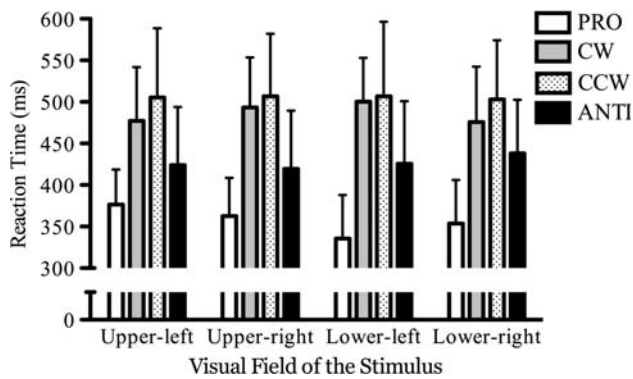
## Data collection and statistical analysis

An infrared emitting diode (IRED) was affixed to the nail of the right index finger and the spatial position of the IRED was sampled at 200 Hz for 1 s via an OPTOTRAK Certus (Northern Digital Inc.; Waterloo, ON, Canada). Displacement data were filtered offline using a second-order dual-pass Butterworth filter with a low-pass frequency of 15 Hz. Instantaneous velocities were obtained by differentiating displacement data via a three-point central finite difference algorithm. Movement onset was defined as the first frame in which resultant velocity exceeded 50 mm/s for ten consecutive frames (i.e., 50 ms) and movement offset was defined as the first of ten consecutive frames in which velocity was <50 mm/s. Dependent variables included: RT (the time from the onset of the target stimulus to movement onset), variable RT (VRT: within-participant standard deviations of RT) and movement time (MT: time from movement onset to movement offset). Dependent measures were subjected to 4 (task: PRO, ANTI, CW, CCW) × 2 (amplitude: near, far) fully repeated measures analysis of variance.<sup>1</sup> In line with our previous work (Neely and Heath 2009), we conducted six pairwise comparisons when a main effect of task was revealed. All other significant main effects and interactions were decomposed via simple effects analyses ( $P < 0.05$ ).

## Results

The results for RT and VRT revealed effects for task,  $F_s(3,42) = 97.81$  and 25.49, respectively, for RT and VRT,  $P_s < 0.001$  (see Fig. 2). The PRO task yielded faster (357 ms SD 46) and less variable (44 ms SD 13) response latencies than the ANTI task (RT = 427 ms SD 68; VRT = 55 ms SD 15), which, in turn, produced faster and less variable RTs than the CW (RT = 487 ms SD 57;

<sup>1</sup> We did not include visual field in our analysis of variance because our previous work demonstrated that RTs for task (i.e., PRO, ANTI, CW, CCW) are not influenced by stimulus location (Neely and Heath 2009). To highlight this point, Fig. 2 depicts RT as a function of task and visual field. This figure demonstrates that RT results in the present investigation were consistent across each visual field.



**Fig. 2** Mean reaction time (ms) as a function of task (*PRO*, *CW*, *CCW*, *ANTI*) and visual field of the target stimulus. Although not included in our ANOVA model, we depict task as a function of visual field to demonstrate that the pattern of results for RT was independent of the location of the target stimulus. Error bars represent one standard deviation

**Table 1** The results for all pairwise comparisons for RT and VRT

Comparison	Dependent variable	
	RT	VRT
PRO versus CW	$t(14) = -19.60, P < 0.001$	$t(14) = -5.28, P < 0.001$
PRO versus CCW	$t(14) = -12.48, P < 0.001$	$t(14) = -6.85, P < 0.001$
PRO versus ANTI	$t(14) = -7.60, P < 0.001$	$t(14) = -4.10, P < 0.001$
ANTI versus CW	$t(14) = -5.99, P < 0.001$	$t(14) = -2.79, P = 0.015$
ANTI versus CCW	$t(14) = -10.40, P < 0.001$	$t(14) = -5.38, P < 0.001$
CW versus CCW	$t(14) = -1.72, P = 0.108$	$t(14) = -3.01, P < 0.009$

VRT = 66 ms SD 12) and CCW tasks (RT = 506 ms SD 78; VRT = 81 ms SD 19) (for all pairwise comparisons see Table 1).

The results for MT yielded effects for task,  $F(3,42) = 3.84, P = 0.016$ , and amplitude,  $F(1,14) = 15.40, P = 0.002$ , as well as a task by amplitude interaction,  $F(3,42) = 4.62, P = 0.007$ . PRO (297 ms SD 62) and ANTI (328 ms SD 96) reaches to the near amplitude were faster than reaches to the far amplitude (PRO = 313 ms SD 66; ANTI = 335 ms SD 94) [ $ts(14) = -6.75$  and  $-3.03$ , for PRO and ANTI, respectively,  $Ps < 0.01$ ]. In contrast, CW and CCW reaches to the near (CW = 321 ms SD 90; CCW = 332 ms SD 91) and far amplitudes were equivalent (CW = 327 ms SD 98; CCW = 336 ms 93) [ $ts(14) = -1.57$  and  $-1.31$ , respectively,  $Ps > 0.05$ ].

## Discussion

The first issue to address is the finding that PRO responses were initiated faster than ANTI, CW and CCW responses. This finding is in line with a myriad of studies that have shown that tasks entailing direct compatibility between a

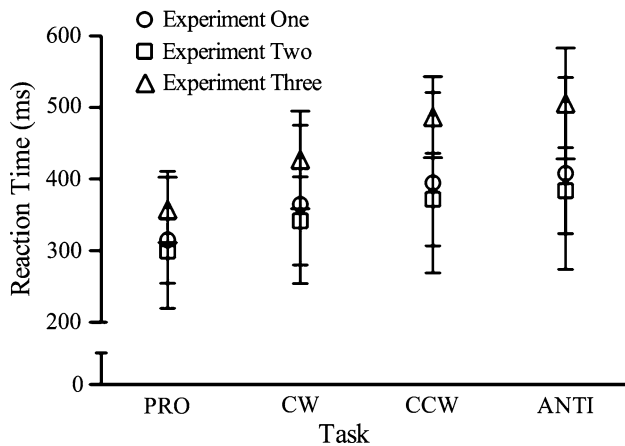
visual stimulus and a motor response are mediated by stimulus-driven visuomotor networks residing in the dorsal visual pathway in the posterior parietal cortex (Milner and Goodale 1995). Importantly, visuomotor networks have been shown to rapidly map response parameters (e.g., Rossetti et al. 2005) independent of awareness of stimulus properties (Binsted et al. 2007; Heath et al. 2008). In other words, dimensional overlap between stimulus and response optimizes the speed of movement planning.

A second and more principal issue to the present study is the finding that the RT advantage for the ANTI task was not influenced by perceptual expertise with the cardinal axes. Recall that Purves and colleagues have demonstrated that percepts are derived via past perceptual experience (Howe et al. 2006). Thus, in line with Purves and colleagues' work, we reasoned that perceptual experience might influence the cognitive processes mediating VMR tasks. Specifically, deriving the egocentric location of the target stimulus or movement endpoint may be optimized when they occur along the same cardinal axis. In contrast, when stimuli are presented along less familiar planes, the computational demands of response preparation may be influenced to such an extent that RT differences between the ANTI, CW, and CCW tasks are attenuated. In discussing the present study, it is therefore noteworthy to contrast response latencies from the current study with those of our earlier work (Neely and Heath 2009). As shown in Fig. 3, examination of RT between experiments revealed that response latencies associated with target stimuli appearing in the cardinal axes were faster than those associated with target stimuli that appear in less familiar locations in the visual field [ $F(2,44) = 5.79, P = 0.006$ ].<sup>2</sup> In other words, perceptual expertise affords an advantage for response preparation when the target stimulus and movement endpoint are congruent with the cardinal axes. More importantly, however, the present results demonstrate that this response planning advantage does not influence the computational differences associated with response preparation for the VMR tasks studied here; that is, PRO responses were faster and less variable than ANTI responses, which, in turn were faster and less variable than CW and CCW responses. Such findings demonstrate that the RT advantage for ANTI responses is not limited to situations wherein the visual stimulus and motor output are congruent with the cardinal axes.

The present work, in concert with our previous investigation (Neely and Heath 2009), demonstrates that ANTI,

<sup>2</sup> Mean RT were submitted to a 3 (Experiment: Experiment 1, Neely and Heath 2009; Experiment 2 Neely and Heath 2009; Experiment 3)  $\times$  4 (task: PRO, ANTI, CW, CCW) split-plot analysis of variance. Importantly, only right-hand trials from Experiments 1 and 2 were included in this analysis.





**Fig. 3** Mean reaction time (ms) as a function of task (*PRO*, *CW*, *CCW*, *ANTI*) and experiment (Experiment 1, Neely and Heath 2009; Experiment 2, Neely and Heath 2009; Experiment 3, the present experiment). Note: target stimuli were presented along the *vertical* and *horizontal* meridians in Experiments 1 and 2, respectively. Error bars represent one standard deviation

*CW* and *CCW* tasks are not universally mediated by the imagined rotation of the movement vector. This finding is counter to the *mental rotation model* advanced by Georgopoulos and Massey (1987); however, our results are in accord with Cisek and colleagues' theory of gradual response substitution (Cisek and Scott 1999; Cisek and Kalaska 2005). Specifically, Cisek and Scott (1999) and Cisek and Kalaska (2005) have shown that multiple population vectors are elicited when multiple reaching directions are possible. In the VMR task, Cisek and Scott (1999) suggest that two population vectors are generated at stimulus onset, one representing the direction of the stimulus and another reflecting the direction of the motor response. Through a process of response substitution, the stimulus vector decays while the movement vector reaches threshold for movement initiation. Importantly, this notion of response-replacement suggests that response latencies may not be determined by the instructed angle of rotation.

We believe our RT data are evidence of a similar response-replacement process. Specifically, we posit that the tasks investigated here invoke a serial process requiring suppression of a stimulus-driven and automatically generated motor plan, followed by the production of a voluntary (and thus cognitively mediated) response to an alternate location (Heath et al. 2009a, b; Neely and Heath 2009). During a block of *ANTI*, *CW*, or *CCW* trials, the onset of the target stimulus may elicit the generation of population vectors in the direction of the stimulus, as well as in the direction of the voluntary response. Given this prediction, the RT values observed here are interpreted as an analog of the time required for the initial stimulus-driven response to decay and the movement vector to exceed threshold for initiation of the voluntary motor response. Further, the degree

of similarity between the stimulus-driven and voluntary responses influences this processes. When the stimulus-driven and voluntary responses occur within the same movement plane (e.g., the *ANTI* task), the complexity of the remapping process is reduced relative to conditions in which the stimulus-driven and voluntary responses lie in orthogonal movement planes (e.g., the *CW* and *CCW* tasks). More specifically, the *ANTI* task simply requires the inversion of the initial stimulus vector, a process that is cognitively less demanding than the computation of a movement vector in an orthogonal direction. Indeed, electrophysiological and neuroimaging studies have demonstrated that the anti-saccade task is mediated by a similar process of vector inversion (Moon et al. 2007; Zhang and Barash 2004; for a review see Munoz and Everling 2004). Further, there is some work in the mental rotation literature which suggests a RT advantage for orientations of  $180^\circ$  relative to intermediate orientations and that the cognitive processes supporting such activities are an analog to the vector inversion process characterizing the *ANTI* task (Jolicoeur 1992; Lawson and Jolicoeur 2003; Murray 1997; for a review see Jolicoeur 1990). Taken together, the aforementioned anti-saccade and mental rotation studies, along with our work, provide evidence for the use of a vector inversion strategy in the *ANTI* task. Such a strategy is cognitively less demanding than the computation of a movement vector in a direction orthogonal to the stimulus.

Our MT findings provide further evidence of computational differences between the *ANTI*, *CW* and *CCW* tasks. Recall that MTs scaled to target amplitude when responses were in the same plane as the target stimulus (i.e., *PRO*, *ANTI*), but not when responses were orthogonal to the target stimulus (i.e., *CW*, *CCW*). Such results suggest that the perceptual representation supporting the *CW* and *CCW* tasks is less stable than that supporting the *PRO* and *ANTI* tasks. Such a finding is in line with the notion that visuomotor uncertainty diminishes the extent to which response parameters are mapped to the metrical properties (i.e., amplitude) of a stimulus (Heath 2005).

It is important to note that the present work does not equivocally determine whether VMR for angles other than  $180^\circ$  is mediated via a mental rotation strategy. Thus, there are two explanations for the present results. On the one hand, it is possible that the *ANTI* task was supported by a vector inversion strategy whereas the *CW* and *CCW* tasks were supported by a mental rotation strategy. On the other hand, it is possible that response preparation was not mediated via a mental rotation strategy for any of the VMR tasks investigated (i.e., *ANTI*, *CW*, *CCW*). The present work cannot disentangle these explanations. Importantly, however, the present study, in concert with our previous investigation (Neely and Heath 2009), provides emergent evidence to assert that response latencies in the *ANTI*, *CW*

and CCW tasks are not similarly mediated by a mental rotation strategy. Thus, future investigations should evaluate a variety of instruction angles to determine the cognitive strategies that mediate response preparation in the VMR task.

## Conclusions

Reaction times were faster and less variable for the PRO task, followed by the ANTI task, which, in turn, were faster and less variable than the CW and CCW tasks. This finding confirms that the RT advantage for the ANTI task is not exclusive to situations wherein the visual stimulus and motor output are congruent with the cardinal axes. We interpret our data as evidence of a serial process characterizing response preparation: an initial stimulus-driven response must be suppressed while a voluntary and task-appropriate response is generated. We believe that the requisite sensorimotor transformations that mediate this process are cognitively less demanding when the stimulus-driven and voluntary responses occur in the same movement plane. More specifically, we contend that the ANTI task requires the inversion of the initial stimulus vector, a process that is cognitively less demanding than the computation of a movement vector in a direction orthogonal to the stimulus.

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