



Visuomotor mental rotation: Reaction time is not a function of the angle of rotation

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ABSTRACT

The goal of the present investigation was to determine whether the anti-pointing task (i.e., pointing to a location 180° from a visual cue [M. Heath, A. Maraj, A. Gradkowski, G. Binsted, Anti-pointing is mediated by a perceptual bias of target location in left and right visual space, *Exp. Brain Res.* 192 (2009) 275–286]) and a 90°-rotated-pointing task are supported by a similar cognitive strategy. Previous work evaluating visuomotor mental rotation (MR) has reported a monotonic increase in reaction time (RT) as a function of the angle of rotation [A.P. Georgopoulos, G. Pellizzer, The mental and the neural: psychological and neural studies mental rotation and memory scanning, *Neuropsychologia* 33 (1995) 1531–1547]. Interestingly, however, anti-pointing movements have not been evaluated in concert with intermediary angles of rotation. We therefore examined RT for center-out pointing movements in four tasks: pro-pointing (PRO), anti-pointing (ANTI), and 90° clockwise (CW90) and counter-clockwise (CCW90) pointing. We found that response latencies for PRO responses were faster than ANTI responses, which in turn were faster than CW90 and CCW90 responses. These findings counter the notion that the angle of rotation influences the speed of visuomotor MR. Instead, we posit that visuomotor MR is supported by a serial process requiring the suppression of a stimulus-driven response followed by voluntary response generation. Further, we suggest that preparation of the voluntary response is cognitively less demanding for the ANTI task because the sensorimotor transformations underlying such an action are completed within the same plane as the stimulus-driven response. In contrast, the cognitive demands associated with CW90 and CCW90 are more complex because the action requires the transformation of response parameters in a movement plane orthogonal to the original – and suppressed – stimulus-driven response.

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Mental rotation (MR) is a cognitive process wherein an object is rotated about a given axis in two- or three-dimensional space. Shepard and Metzler [27] first described this psychological operation in an elegant series of experiments designed to evaluate the cognitive demands characterizing MR. Their experimental paradigm required participants to decide if two tachistoscopically presented line drawings were identical. The results were compelling: the time required to make a decision was linearly related to the angular difference between the two objects, suggesting that participants mentally rotated one of the objects through increasing angles of rotation until a decision was made. MR has thus been characterized as an analog process in which reaction time (RT) is linearly related to the angle of rotation. A plethora of work in the cognitive neurosciences has confirmed this finding and extended it to the MR of alphanumeric characters [8], novel shapes, cubes and poly-

gons [6,7], and drawings of body parts [9,24]. Subsequent functional neuroimaging studies have demonstrated consistent activation in posterior parietal and posterior frontal cortices during MR tasks (e.g., [4], for a review see [29]) and the degree and extent of activation in these areas has been shown to be related to the cognitive demands of the task (for a review see [29]). Together, the neurophysiological and behavioral findings described above demonstrate that the cognitive processes mediating MR are measurable and that motor areas play a key role in supporting this non-motor task.

The MR literature has further been extended to describe the cognitive processes mediating visuomotor MR for eye [11,12] and hand movements [14,26] (for a review see [15]). Visuomotor MR requires the spatial remapping of a visual cue to a location corresponding to a predetermined angular departure. Interestingly, Pellizzer and Georgopoulos [26] demonstrated that the computational demands of visuomotor MR and classic MR tasks were correlated, suggesting that a common cognitive strategy underlies performance in both tasks. In their visuomotor task, Georgopoulos and colleagues [14,26] investigated angles of 0°, 5°, 10°, 15°, 35°, 70°, 105° and 140°. In accord with the MR literature, they reported an increase in RT as a function of the angle of rotation; suggesting visuomotor

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MR is mediated by the imagined rotation of the movement vector about its origin. Moreover, neurophysiological studies involving nonhuman primates have revealed that the direction of the neural population vector in primary motor cortex is gradually rotated over time, from the location of the stimulus to the direction of the to-be-completed motor response [10,13,19].

One potential limitation of the visuomotor MR literature is that angles of greater than 140° have not been evaluated in concert with intermediary angles. Thus, it is unclear whether the monotonic increase in RT can be extrapolated beyond 140° . A second limitation is that previous visuomotor studies have not explicitly contrasted the cognitive demands of MR in clockwise and counter-clockwise directions. This represents a notable issue in light of work suggesting that the cognitive demands of clockwise rotation are reduced relative to counter-clockwise rotation [3]. The present work therefore sought to extend Georgopoulos and colleagues' [14,26] visuomotor MR work to determine if rotations of 180° are supported by a MR strategy. Further, we sought to determine whether the direction of rotation influences the cognitive demands of response preparation. To that end, participants completed center-out pointing movements in four tasks: pro-pointing, anti-pointing (i.e., pointing to a location 180° from a visual cue [16,17]), and 90° clockwise and counter-clockwise rotated-pointing. Target stimuli were presented along the vertical (Experiment One) and horizontal (Experiment Two) meridians. Importantly, we prohibited eye movements because it has been suggested that horizontal gaze provides more precise information to the motor system than vergence [5]. If anti- and rotated-pointing are supported by imagined rotation of the movement vector, then response latencies for anti-pointing will be longer and more variable than those for pointing to an intermediate angle. On the other hand, it is possible that anti-pointing is cognitively less demanding than 90° -pointing because the sensorimotor transformations underlying automatic response suppression and voluntary response generation are completed within the same movement plane. That is, if the anti- and 90° -pointing tasks are mediated by a serial process in which a stimulus-driven motor plan must be suppressed and then recomputed to support the appropriate response, then the complexity of the remapping process will be reduced for anti-pointing in comparison to 90° -pointing. As a result, anti-pointing responses will elicit faster and less variable reaction times than 90° -pointing counterparts.

Sixteen participants (6 male; 18–29 years of age) volunteered in Experiment One and an equal number of different participants (5 male; 18–24 years of age) volunteered in Experiment Two. Participants were naïve to the hypothesis being tested, were self-declared right-hand dominant, and had self-declared normal or corrected-to-normal vision. All work was conducted in accord with the ethical standards laid down in the 1964 Declaration of Helsinki and all procedures were carried out with the understanding and written consent of the participants.

Participants were seated at a virtual aiming apparatus for the duration of the experiment (for schematic of the apparatus see [23]). The top shelf of the apparatus supported a monitor (DELL: 1707FP, 8 ms response rate; Austin, TX, USA) placed upside down to project visual stimuli onto a one-way mirror, which composed the middle shelf of the apparatus. Reaching movements were completed underneath the one-way mirror on a table-top surface, which composed the bottom shelf of the apparatus. The distance between the top shelf and middle shelf, and the middle shelf and the bottom shelf was 34 cm, thus, the optical geometry was such that stimuli projected on the mirror were perceived as being located on the table-top surface. The room lights in the experimental suite were extinguished for the duration of the testing session and as a result, the one-way mirror occluded direct vision of the limb. Eye movements were monitored by the experimenter via a 120 Hz video-based eye-tracking system (Applied Science Laboratories: H6

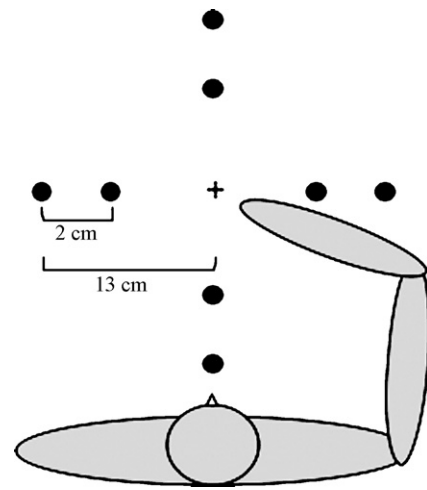


Fig. 1. Bird's eye view of the stimulus configuration. In Experiment One, one of two target stimuli, 11 and 13 cm from the fixation point, was presented in either the upper or lower visual field in each trial. In Experiment Two, one of two target stimuli, 11 and 13 cm from the fixation point, was presented in either the left or right visual field in each trial. Reaching trajectories were completed in all four visual fields.

HS CN; Bedford, MA, USA) and participants' midline was centered on the viewing area. All experimental events were controlled via MATLAB (The MathWorks; Natick, MA, USA) and Psychophysics Toolbox extensions [2,25].

Stimuli included a white fixation cross (10 mm by 10 mm) and eight white target stimuli (10 mm diameter circles) all of which were presented against a high-contrast black background. 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). Therefore participants had veridical information about the spatial position of the limb at the beginning of each trial. Target stimuli were located at two eccentricities, 11 and 13 cm from the fixation point (see Fig. 1) and are henceforth referred to as near and far, respectively. At the start of all trials, participants were instructed to direct their gaze, and place their finger, on the start position fixation cross. Participants were instructed to maintain gaze fixation for the duration of the trial. After 1000 ms, a stimulus was presented for 50 ms in one of four possible locations (see below). The onset of the stimulus served as the movement initiation cue.

Participants completed four pointing 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 clockwise (CW90) and a counter-clockwise (CCW90) rotation task in which they pointed to a location 90° clockwise or counter-clockwise to the target stimulus. In Experiment One, target stimuli were projected in the upper and lower visual fields. Thus, PRO and ANTI responses were completed in the same plane as the target stimuli (i.e., the anteroposterior axis) with the former being directed to the veridical location of the target stimulus and the latter directed to a location 180° from the target stimulus. For CW90 and CCW90, responses were orthogonal to the location of the stimulus; i.e., responses were directed in left and right visual fields (i.e., the mediolateral axis). In Experiment Two, target stimuli were projected in the left and right visual fields. Hence, PRO and ANTI responses were completed in the same movement plane as the target stimuli (i.e., the mediolateral axis). In contrast, CW90 and CCW90 responses were orthogonal to the location of the stimulus (i.e., the anteroposterior axis). 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

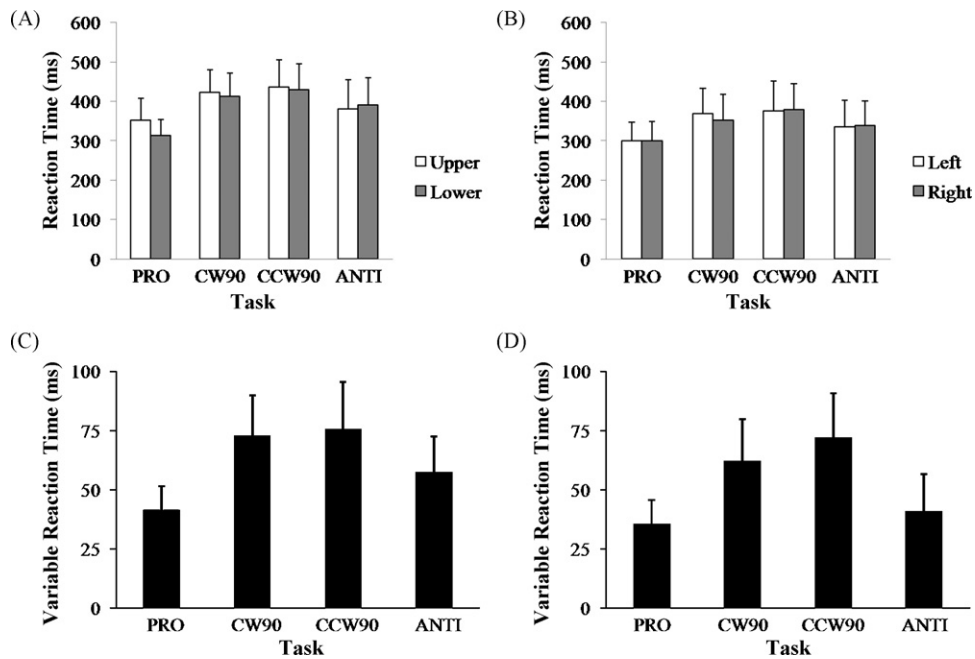


Fig. 2. (A) Mean reaction time (ms) as a function of task (PRO, CW90, CCW90, ANTI) and stimulus location (upper visual field, lower visual field) in Experiment One. (B) Mean reaction time (ms) as a function of task (PRO, CW90, CCW90, ANTI) and stimulus location (left visual field, right visual field) in Experiment Two. (C) Mean variable reaction time (ms) as a function of task for Experiment One and (D) Experiment Two. Error bars represent one standard deviation.

location and stimulus eccentricity was randomized within each block of trials. Participants completed the above protocol with both the left and right hands (performed in separate blocks) and starting limb was counterbalanced across participants. In total, participants completed 320 trials in an experimental session.

An infrared emitting diode (IRED) was affixed to the nail of the 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 10 consecutive frames (i.e., 50 ms) and movement offset was defined as the first of 10 consecutive frames in which velocity was less than

50 mm/s. Dependent variables included: reaction time (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 variables from Experiments One and Two were examined independently and each variable was subjected to 2 (hand: left, right) by 4 (task: PRO, ANTI, CW90, CCW90) by 2 (stimulus location: upper, lower (Experiment One) or left, right (Experiment Two)) by 2 (stimulus eccentricity: near, far) fully repeated measures analysis of variance. Significant main effects and/or interactions ($p < 0.05$) were decomposed via simple effects or pairwise comparisons as appropriate. Because this was the first investigation directly comparing pro-pointing with 90° and 180° rotated-pointing, we elected to conduct six pairwise comparisons when a main effect of task was revealed.

The results for RT in Experiments One and Two revealed main effects of task, $F_s(3, 45) = 60.86$ and 63.02 , respectively, $ps < 0.001$, and interactions for task by stimulus location, $F_s(3, 45) = 14.13$ and 4.14 , respectively, $ps < 0.01$ (see Fig. 2). In addition, Experiment One yielded a main effect of stimulus location, $F(1, 15) = 16.62$, $p < 0.001$. We decomposed the above interactions by examining the impact of task separately for each stimulus location. The results of these analyses revealed main effects of task for each stimulus location ($ps < 0.001$): PRO responses elicited the fastest RTs, followed by ANTI responses, which were faster than CW90 and CCW90 responses. CW90 and CCW90 responses were generally found to elicit comparable RTs with the exception that CW90 responses in Experiment One were faster than CCW90 when the target stimulus appeared in the right visual field (see Table 1 for pairwise comparisons). The analysis of VRT for Experiments One and Two yielded main effects of task, $F_s(3, 45) = 39.74$ and 52.96 , respectively, $ps < 0.001$ (see Fig. 2). VRT increased from PRO to ANTI responses and again from ANTI to CW90 and CCW90 responses. CW90 and CCW90 responses exhibited equivalent variability in Experiment One whereas the former exhibited decreased variability in comparison to the latter in Experiment Two (see Table 2 for pairwise comparisons).

The results for MT in Experiments One and Two revealed main effects of stimulus eccentricity, $F_s(1, 15) = 33.08$ and 49.01 , respec-

Table 1
The results for all pairwise comparisons between tasks for reaction time.

Comparison	Visual field	
	Upper	Lower
A. Experiment One		
PRO vs. CW90	$t(15) = -7.70, p < 0.001$	$t(15) = -12.95, p < 0.001$
PRO vs. CCW90	$t(15) = -7.51, p < 0.001$	$t(15) = -10.71, p < 0.001$
PRO vs. ANTI	$t(15) = -6.25, p < 0.001$	$t(15) = -12.29, p < 0.001$
ANTI vs. CW90	$t(15) = -4.21, p = 0.001$	$t(15) = -3.11, p = 0.007$
ANTI vs. CCW90	$t(15) = -5.05, p < 0.001$	$t(15) = -4.46, p < 0.001$
CW90 vs. CCW90	$t(15) = -1.79, p = 0.094$	$t(15) = -1.66, p = 0.119$
Comparison	Visual field	
	Left	Right
B. Experiment Two		
PRO vs. CW90	$t(15) = -8.56, p < 0.001$	$t(15) = -6.47, p < 0.001$
PRO vs. CCW90	$t(15) = -10.52, p < 0.001$	$t(15) = -11.24, p < 0.001$
PRO vs. ANTI	$t(15) = -6.03, p < 0.001$	$t(15) = -6.70, p < 0.001$
ANTI vs. CW90	$t(15) = -5.18, p < 0.001$	$t(15) = -2.28, p = 0.038$
ANTI vs. CCW90	$t(15) = -5.31, p < 0.001$	$t(15) = -6.17, p < 0.001$
CW90 vs. CCW90	$t(15) = -1.05, p = 0.311$	$t(15) = -4.03, p = 0.001$

Table 2

The results for all pairwise comparisons between tasks for variable reaction time.

Comparison	Experiment One	Experiment Two
PRO vs. CW90	$t(15) = -11.38, p < 0.001$	$t(15) = -8.07, p < 0.001$
PRO vs. CCW90	$t(15) = -9.92, p < 0.001$	$t(15) = -9.17, p < 0.001$
PRO vs. ANTI	$t(15) = -12.34, p < 0.001$	$t(15) = -2.24, p = 0.040$
ANTI vs. CW90	$t(15) = -4.16, p < 0.001$	$t(15) = -12.96, p < 0.001$
ANTI vs. CCW90	$t(15) = -5.11, p < 0.001$	$t(15) = -7.67, p < 0.001$
CW90 vs. CCW90	$t(15) = -1.85, p = 0.427$	$t(15) = -2.52, p = 0.024$

tively, $ps < 0.001$, and interactions for hand by task by stimulus location, $F_s(3, 45) = 6.97$ and 5.76 , respectively, $ps < 0.01$. MTs were faster for the near stimulus (314 ms SD66 and 313 ms SD75, for Experiments One and Two, respectively) than for the far stimulus (323 ms SD68 and 323 ms SD74, for Experiments One and Two, respectively). As expected, both experiments showed that MTs for the left and right hands were faster for reaches in ipsilateral than contralateral space ($ps < 0.01$). In turn, MTs for reaches in the upper and lower visual fields were equivalent ($ps > 0.05$).

The present study sought to determine if anti- and rotated-pointing are mediated by a similar cognitive strategy and whether the direction of rotation influences the cognitive demands of response preparation. Importantly, we provide the first study to contrast the computational demands associated with 90° and 180° rotated-pointing responses. The results demonstrated that PRO responses were initiated faster than rotated-pointing responses: a finding consistent with the notion that responses entailing spatial overlap between a target and a response are mediated by fast and stimulus-driven visuomotor networks (for a review see [20]). In turn, ANTI responses were initiated faster than CW90 and CCW90 responses: a finding indicative of the fact that the computational demands associated with 180° rotation were less than those of 90° rotation. Notably, our results cannot be explained by biomechanical differences as evidenced by the fact that CW90 and CCW90 responses elicited slower RTs than ANTI responses regardless of the responding hand as well as whether the response was completed in the anteroposterior or mediolateral plane. Instead, we propose that remapping the stimulus vector to the appropriate movement vector is cognitively more demanding in the CW90 and CCW90 tasks because the requisite sensorimotor transformations require the integration of response parameters in a movement plane that is orthogonal to a stimulus-driven response. In contrast, the sensorimotor transformations associated with the ANTI task are contained within the same plane – albeit in an inverted direction – relative to a stimulus-driven response (i.e., the anteroposterior plane in Experiment One and the mediolateral plane in Experiment Two). This computational difference is evidenced by the finding that ANTI responses elicited faster and less variable RTs relative to CW90 and CCW90 responses. In terms of MT, we found that the left and right hands elicited faster MTs when reaching to targets in ipsilateral space, whereas MTs for midline reaches were equivalent (for discussion of this issue see [1]).

In the anti-saccade task, as well as the visuomotor MR task, early cortical activity initially reflects the location of the stimulus and gradually shifts over time to the direction of the upcoming response [10,13,19,21,28,30,31]. It has been suggested that this early stimulus-driven activity reflects an automatically generated motor plan [18,30,31]. When direct stimulus–response mapping is appropriate for the task, this motor plan supports a fast and effective motor response. In contrast, when the task requires spatial remapping, the initial motor plan must be suppressed and recomputed to support the appropriate response. Electrophysiological and neuroimaging studies have shown this is the case for the anti-saccade task (for a review see [22]); similarly, single-cell recordings in primary motor cortex support the notion that visuomotor MR is supported by a process of automatic response suppression fol-

lowed by voluntary response generation [10,13,19]. The present study evaluated the complexity of the spatial remapping process mediating voluntary response generation. Our findings suggest that this process is influenced by the degree of similarity between the stimulus-driven and voluntary responses. Specifically, in the ANTI task, both responses occur in the same movement plane whereas the CW90 and CCW90 tasks require spatial remapping in a movement plane orthogonal to the stimulus-driven response. We therefore suggest that a spatial remapping process requiring the integration of response parameters in orthogonal movement planes is computationally more demanding than sensorimotor transformations contained within the same movement plane. This computational difference is evidenced by slower and more variable response latencies for the CW90 and CCW90 tasks. Importantly, our findings demonstrate that the ANTI, CW90 and CCW90 tasks are not similarly supported by the imagined rotation of the movement vector. Instead, we propose that the complexity of the spatial remapping process mediating voluntary response generation is of greater influence on RT than the angle of rotation.

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