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The Visuomotor Mental Rotation Task: Visuomotor Transformation Times Are Reduced for Small and Perceptually Familiar Angles

Kristina A. Neely [a] & Matthew Heath [b]

[a] Department of Kinesiology and Nutrition , University of Illinois at Chicago , Chicago, Illinois

[b] School of Kinesiology , The University of Western Ontario , London, Ontario
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RESEARCH ARTICLE

The Visuomotor Mental Rotation Task: Visuomotor Transformation Times Are Reduced for Small and Perceptually Familiar Angles

Kristina A. Neely[1], Matthew Heath[2]

[1]Department of Kinesiology and Nutrition, University of Illinois at Chicago, Chicago, Illinois. [2]School of Kinesiology, The University of Western Ontario, London, Ontario.

ABSTRACT. In the visuomotor mental rotation (VMR) task, participants point to a location that deviates from a visual cue by a predetermined angle. This task elicits longer reaction times (RT) relative to tasks wherein the visual cue is spatially compatible with the movement goal. The authors previously reported that visuomotor transformations are faster and more efficient when VMR responses elicit a degree of dimensional overlap (i.e., 0° and 5°) or when the transformation involves a perceptually familiar angle (i.e., 90° or 180°; K. A. Neely & M. Heath, 2010b). One caveat to this finding is that standard and VMR responses were completed in separate blocks of trials. Thus, between-task differences not only reflect the temporal demands of the visuomotor transformations, but also reflect the temporal cost of response inhibition. The goal of this study was to isolate the time cost of visuomotor transformations in the VMR task. The results demonstrated that visuomotor transformations are more efficient and effective when the response entails a degree of dimensional overlap between target and response (i.e., when the angular disparity between the responses is small) or when the transformation angle is perceptually familiar.
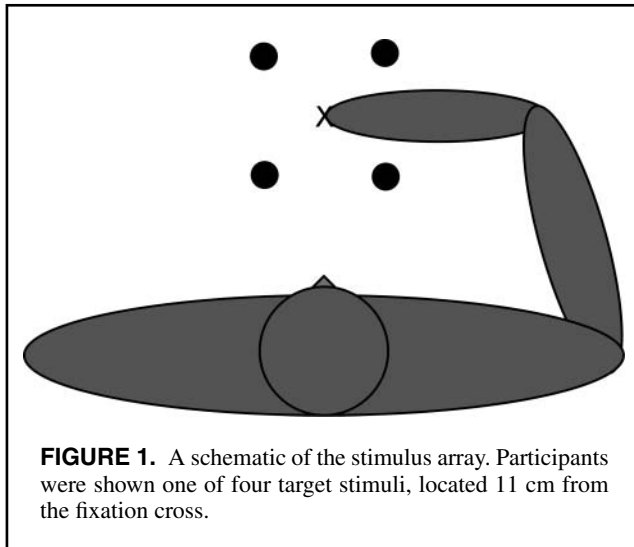
Keywords: rapid aiming movements, response-planning processes, stimulus-response mapping, visuomotor processing

The integration and subsequent transformation of sensory information into motor commands is paramount to successful goal-directed motor behavior. One of the critical factors that influences the efficiency and effectiveness of this process is the spatial compatibility—or the dimensional overlap[1]—between stimulus and response. Motor output is optimized when the visual stimulus is spatially congruent with the movement goal (standard mapping task; Fitts & Seeger, 1952): a finding attributed to the fact that such actions are mediated by fast and stimulus-driven visuomotor networks that operate independent of conscious awareness of the movement goal (Binsted, Brownell, Vorontsova, Heath, & Saucier, 2007; Bridgeman, Lewis, Heit, & Nagle, 1979; Goodale, Pelisson, & Prablanc, 1986; Pisella et al., 2000). In contrast, when a visual stimulus is spatially dissociated from the movement goal (nonstandard mapping task; Wise, di Pellegrino, & Boussaoud, 1996), the normally fast and stimulus-driven nature of visuomotor control is disrupted. An extensively studied nonstandard task is the antisaccade or antipointing task (Chua, Carson, Goodman, & Elliott, 1992; Heath, Maraj, Gradkowski, & Binsted, 2009; Heath, Maraj, Maddigan, & Binsted, 2009; for a review of the antisaccade literature, see Munoz & Everling, 2004). In this task, eye or limb movements are directed to a mirror-symmetrical location relative to the visual cue. The visuomotor mental rotation

(VMR) paradigm is another example of a nonstandard task. In the VMR task, a reaching response is directed to a location that deviates from a visual cue by a predetermined transformation angle (e.g., Georgopoulos & Massey, 1987; Neely & Heath, 2009, 2010a, 2010b; Pellizzer & Georgopoulos, 1993).[2] Nonstandard tasks demonstrate longer reaction times (RT) relative to their standard task counterparts. The increase in RT has been tied to the need for conscious awareness of the movement goal and a visuomotor transformation process mediated by slow cognitive control (Day & Lyon, 2000; Heath, Maraj, Gradowski, et al., 2009; Rossetti et al., 2005).

Neuroimaging studies examining the blood-oxygen-level-dependent (BOLD) activity associated with antisaccades and antipointing report that antimovements are associated with more widespread BOLD activity in the parietal and frontal cortices relative to a standard saccade or pointing task (Connolly, Goodale, DeSouza, Menon, & Vilis, 2000; Curtis & D'Esposito, 2003; DeSouza, Menon, & Everling, 2003; Ford, Goltz, Brown, & Everling, 2005). The increased BOLD activity associated with nonstandard tasks is thought to provide evidence of two additional operations unique to the nonstandard task: (a) the computation and subsequent inhibition of a standard response (i.e., response inhibition), and (b) the computation of a voluntary response to an alternate location in the visual field. In addition to an increase in BOLD activity, the cognitive demands of response inhibition are reflected in the prolonged RTs that characterize nonstandard tasks (Heath, Maraj, Maddigan, et al., 2009; Olk & Kingstone, 2003). In particular, Olk and Kingstone used a paradigm in which pro- and antisaccades were completed in separate blocks and in a mixed block wherein pro- and antisaccades were randomly interleaved on a trial-by-trial basis. Because a priori knowledge related to task type was not available in the mixed block, a comparable level of response inhibition was required for pro- and antisaccades. Olk and Kingstone demonstrated that when equated for response inhibition, a significant reduction in the prosaccade RT advantage is observed. Similarly, work by our group (Heath, Maraj, Maddigan, et al., 2009) reported that the RT difference between pro- and antipointing responses is reduced when the tasks are randomly interleaved.

Correspondence address: Kristina A. Neely, Department of Kinesiology and Nutrition, University of Illinois at Chicago, 1919 West Taylor, 650 AHSB (M/C 994), Chicago, IL 60612, USA. e-mail: kneely@uic.edu

FIGURE 1. A schematic of the stimulus array. Participants were shown one of four target stimuli, located 11 cm from the fixation cross.
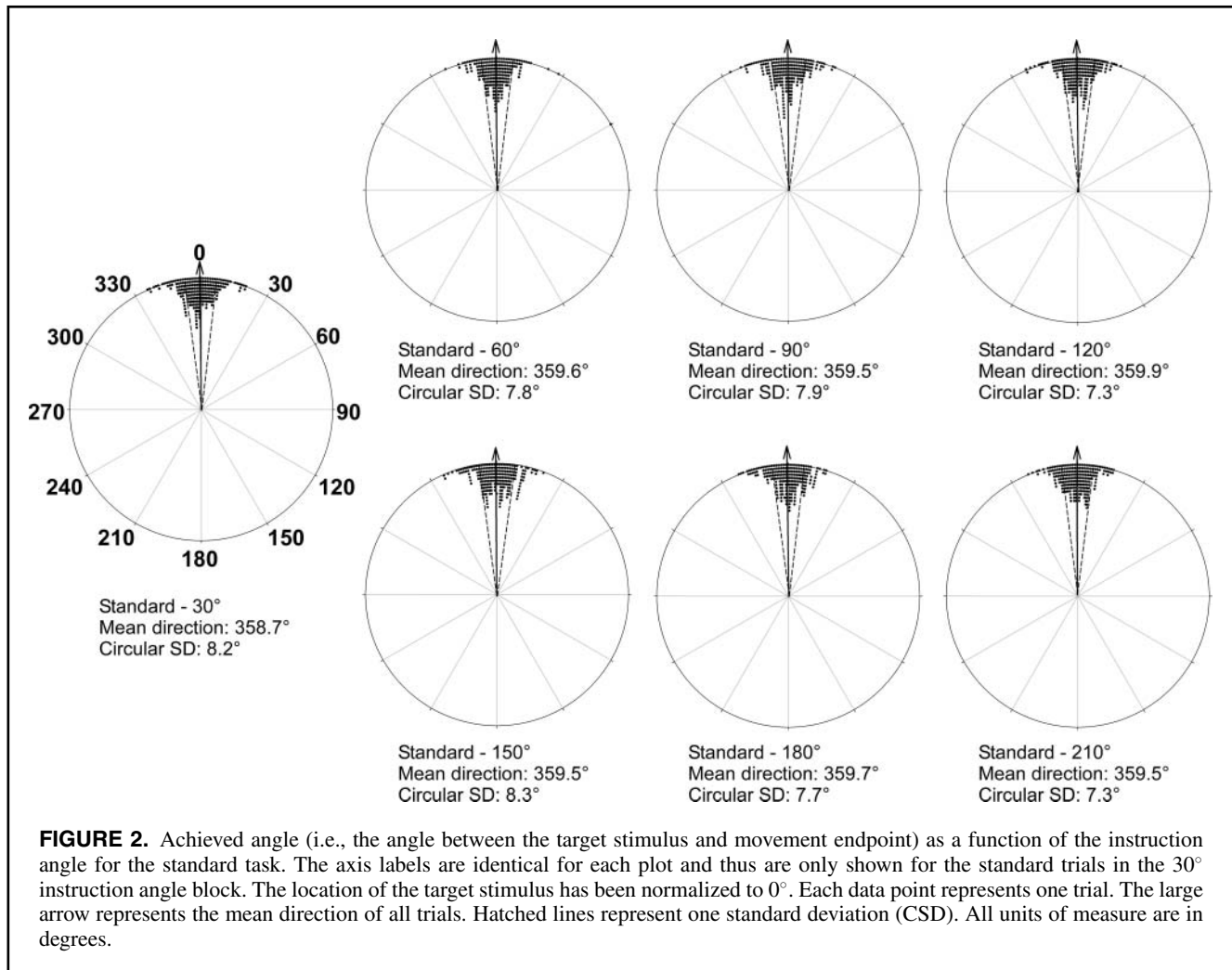
Taken together, these studies demonstrate that the inhibition of a stimulus-driven response represents a measurable and a time-consuming component of the nonstandard task.

Following the inhibition of a standard response, visuo-motor transformations specific to the directional properties of the nonstandard task must be computed. Several theories offer an explanation as to how such transformations are conducted. Prominent among them are the *mental rotation model* (Georgopoulos & Massey, 1987) and the *response substitution hypothesis* (Cisek & Scott, 1999). The mental rotation model asserts that response preparation is mediated by the imagined rotation of a movement vector about its origin. In particular, the vector between the visual stimulus and limb position is computed and then rotated until it reaches the appropriate direction for the response at which point it is translated into motor output. The mental rotation model asserts an analogue process whereby RTs increase linearly as a function of increasing transformation angle for all angles up to and beyond 180°.[3] In contrast, the response substitution hypothesis asserts that the VMR task elicits two distinct neural representations—one representing the standard response and another representing the nonstandard response. Through a process of response substitution, an initial movement plan to the visual stimulus (i.e., the standard response) is replaced with that of the nonstandard response. In this context, response preparation is optimized when the visual stimulus and the movement goal are spatially aligned (see Figure 2A of Cisek & Scott) and increases (in duration) as the distance between the responses increases. In addition, the response substitution hypothesis contends that learned associations between a stimulus and the direction of a response influence the rate of response selection. Thus, RT is not predicted to increase monotonically as a function of increasing transformation angle; rather, the conjoint influence of the angular disparity between stimulus and response and familiarity with

the required movement outcome are thought to influence response planning.

In a series of recent studies (Neely & Heath, 2009, 2010a, 2010b), we examined the behavioral properties that influence RTs in the VMR task. Neely and Heath (2010a) reported two VMR experiments wherein participants completed responses using the same transformation angles employed by Georgopolous and Massey (1987; i.e., Experiment 1: 0°, 5°, 10°, 15°, 35°, 70°, 105°, and 140°) and a set of equally spaced angles (i.e., Experiment 2: 0°, 30°, 60°, 90°, 120°, 150°, 180°, and 210°) that included the perceptually familiar angles of 90° and 180°. Results for Experiment 1 yielded a faithful replication of Georgopoulos and Massey's work: RTs increased linearly with increasing angle of rotation. However, Experiment 2 elicited a nonlinear relationship such that RTs were optimized for trials involving the instruction angles of 30°, 90°, and 180°—a pattern of results that is not predicted by the mental rotation model. We argued that this finding supports the response substitution hypothesis' assertion that visuomotor transformations are faster when a degree of dimensional overlap exists between the neural representations of the standard and nonstandard responses. Further, we argued that the findings for the 90° and 180° transformation angles are consistent with the notion that familiarity between a stimulus and response facilitates the response substitution process. Indeed, the notion that 90° and 180° produce a familiarity effect is supported by the visual perception literature reporting enhanced stability for right angles and straight lines in comparison to acute and obtuse angles (e.g., Howe & Purves, 2005; Nundy, Lotto, Coppola, Shimpi, & Purves, 2000; for classic demonstration, see McFarland, 1968).

One caveat of our previous work (Neely & Heath, 2009, 2010a, 2010b) is that standard and VMR tasks were performed in separate blocks of trials. As a result, participants had advance knowledge as to whether an upcoming trial required a standard or VMR response. Consequently, the reported RT difference between tasks reflects not only the cost of response inhibition, but also the cost, or costs, associated with the visuomotor transformations underlying the formulation of a voluntary response to an alternate location. The goal of the present study was to extend our previous work by isolating the temporal cost of the visuomotor transformations. To that end, in the present study we used a randomized task paradigm wherein the instruction to initiate a standard or VMR response was withheld until shortly after stimulus onset. By randomly interleaving standard and VMR trials, the stimulus-driven response was inhibited on all trials, thereby equating response inhibition for standard and VMR tasks. In turn, by evaluating between-task difference scores (VMR task − standard task) this paradigm provides a framework for determining the temporal costs associated with the visuomotor transformations underlying a range of transformation angles. Thus, and to the best of our knowledge, the present work provides the first examination of the direct costs associated with visuomotor transformations.

FIGURE 2. Achieved angle (i.e., the angle between the target stimulus and movement endpoint) as a function of the instruction angle for the standard task. The axis labels are identical for each plot and thus are only shown for the standard trials in the $30°$ instruction angle block. The location of the target stimulus has been normalized to $0°$. Each data point represents one trial. The large arrow represents the mean direction of all trials. Hatched lines represent one standard deviation (CSD). All units of measure are in degrees.

Method

Participants

Participants were 11 volunteers (6 men and 5 women; age range = 21–28 years) from the University of Western Ontario community. All participants were naive to the hypothesis being tested, were self-declared right-hand dominant, and had self-declared normal or corrected-to-normal vision. This 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.

Apparatus and Procedure

Participants were seated at a virtual aiming apparatus (for a schematic of the apparatus, see Neely & Heath, 2010a) for the duration of the testing session. Visual stimuli were projected from a 30-inch flat panel monitor (Dell 3007WFP; 60 Hz, 8 ms response rate; 1280 × 960 resolution; Round Rock,

TX, USA), which was placed upside down on the top shelf of the apparatus, to a one-way mirror that constituted the middle shelf of the apparatus. Participants completed their reaching movements on the lower shelf of the apparatus, which was a smooth, tabletop surface. The distance between the top shelf and middle shelf, and the middle shelf and the reaching surface, was 34 cm; thus, the optical geometry was such that participants perceived stimuli projected on the mirror as being located on the reaching surface of the apparatus. The lights in the experimental suite were extinguished for the duration of the testing session. As a result, only visual information projected by the computer monitor was visible to participants. A chinrest-mounted eye-tracking system (Applied Science Laboratories: H6 HS CN; Bedford, MA, USA) was centered on the viewing area and was used to stabilize the participant's head position and to monitor eye position (see subsequent discussion). All experimental events were controlled via MATLAB (version 7.6; The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox (version 3.1) extensions (Brainard, 1997; Pelli, 1997).

The starting position of the limb was defined by a tactile cue located at body midline and affixed to the reaching surface (i.e., 25 cm from the front edge of the aiming apparatus). The tactile cue was overlaid with a visual cue (i.e., a fixation cross) that was visible for the duration of each trial. As the starting position of the limb was defined by a tactile and visual cue, participants were able to compute an appropriate internal representation of limb position in advance of each pointing response (Prablanc, Echallier, Jeannerod, & Komilis, 1979). Visual stimuli included four white circular targets (10 mm diameter), and white, green, and red fixation crosses (10 × 10 mm), all of which were presented against a high-contrast black background. As shown in Figure 1, target stimuli were located 11 cm from the start position and at a 45° offset from the horizontal and vertical meridians. Although we previously documented that perceptual expertise with the cardinal axes does not ameliorate the planning advantage for 90° and 180° VMR tasks (Neely & Heath, 2010a), we elected to use targets at 45° offsets to further control for any possible congruency advantage with the cardinal axes.

Each trial began with the onset of a white fixation cross that signaled participants to direct their gaze and align their right index finger (i.e., the pointing finger) with the start position. Following a variable foreperiod (1,000–2,000 ms), one of the four target stimuli appeared in concert with the fixation cross for 50 ms. Immediately following the offset of the target stimuli, a color change of the fixation cross (see subsequent details) signaled participants to initiate their reaching response. To prevent oculomotor information from influencing the ensuing motor response (Bock, 1986; van Donkelaar, 1997), participants were instructed to maintain their gaze on the fixation cross for the duration of each trial. Eye movements were monitored online to ensure compliance with this instruction. Trials involving a directional error of the reaching response, or trials involving a smooth or saccadic eye movement, were removed from the experimental sequence and that trial was re-entered into the randomized trial series. Directional errors were identified by two methods. First, participants were asked to report known directional errors immediately after the trial. Second, movement endpoints were evaluated immediately after each trial by the experimenter. Movement endpoints in the wrong quadrant of the reaching area were determined to be directional errors.[4] Participants were not provided with any feedback about their performance.

Participants completed two tasks: a standard task in which they pointed to the location of the target stimulus and a VMR task in which they pointed to a location that deviated from the target stimulus by a specified angle. Tasks were signaled by a color change of the fixation cross. Specifically, a white-to-green change signaled a standard response, whereas a white-to-red change signaled a VMR response. Participants were instructed that all VMR responses should be in a clockwise direction from the target stimulus. Trials were blocked by transformation angle (30°, 60°, 90°, 120°, 150°, 180°, and 210°), and in advance of each block participants were provided with a block instruction screen specifying the transformation angle for the upcoming block of trials. For example, in the block of trials associated with the 30° instruction angle, participants pointed directly to the target stimulus in response to a green fixation cross (i.e., standard trial), whereas they pointed to a location 30° clockwise from the target stimulus in response to a red fixation cross (i.e., VMR trial). In accord with our previous work (Neely & Heath, 2009, 2010a, 2010b), the instruction screen preceding each block provided written instructions and a pictorial representation (i.e., a line drawing) of the instruction angle. The origin of the line drawing was consistent with the center of the visual field and the polar (i.e., reference) axis was consistent with the positive x-axis.
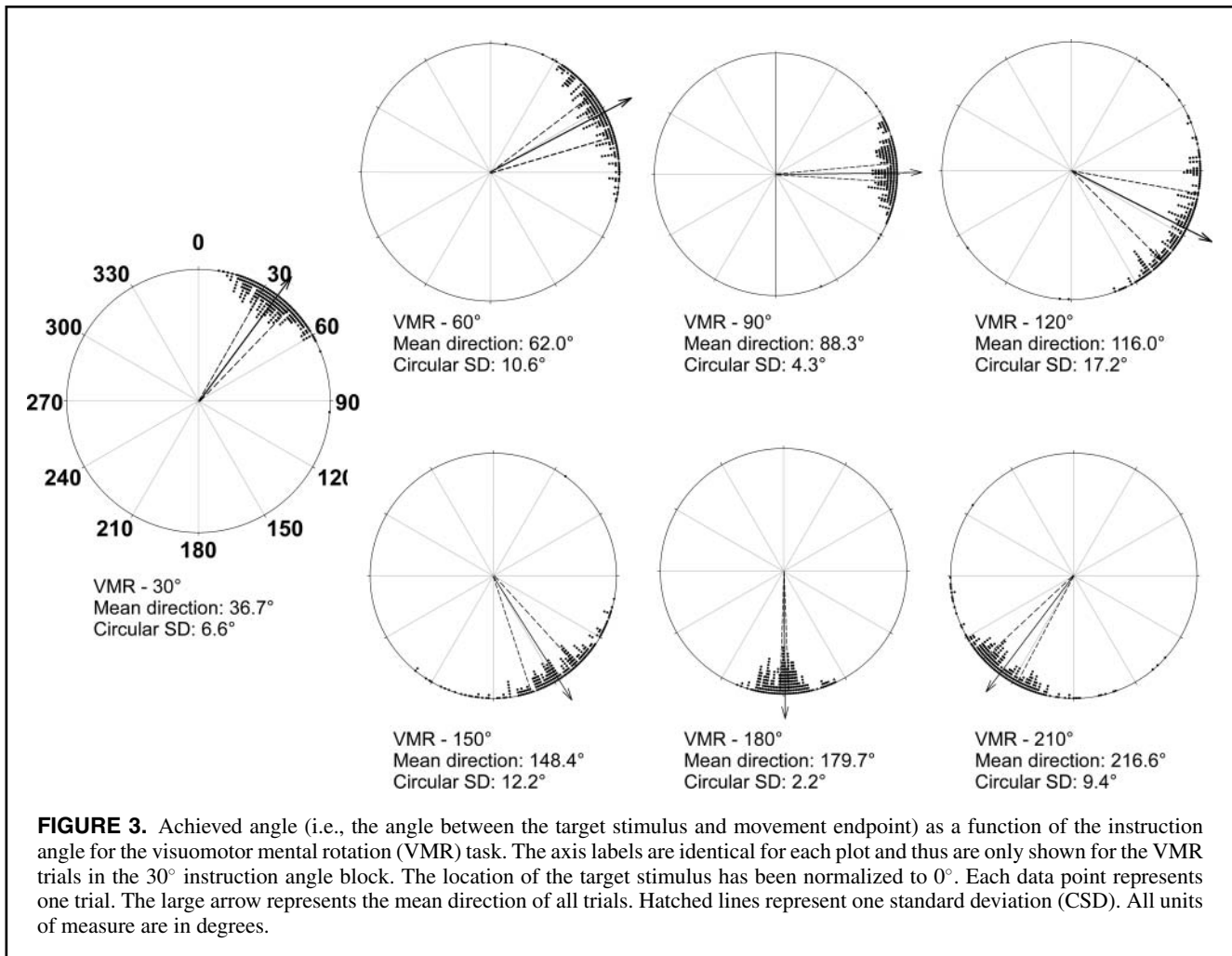
The transformation angle blocks were randomly ordered and within each block the presentation of stimulus location and task type was randomized. Within each of the instruction angle blocks (30°, 60°, 90°, 120°, 150°, 180°, and 210°), five trials were completed to each target stimulus location (location: upper left, upper right, lower left, lower right) and task type (standard, VMR) combination for a total of 40 trials per block. It is important to note that participants were informed that standard and VMR trials were randomly interleaved within each instruction block and that they would complete an equal number of each trial type within a block.

All participants completed a brief training session in advance of the testing session. The procedures for the training session were identical to those of the testing session with two exceptions: the number of trials and the availability of visual feedback. Specifically, participants completed seven blocks (instruction angles of 30°, 60°, 90°, 120°, 150°, 180°, and 210°) of two trials in the practice session, for a total of 14 trials. The practice session took approximately 15 min to complete and was immediately followed by the testing session. The purpose of the practice session was to familiarize participants with the instruction angles as well as the timeline of events within a trial.

An infrared emitting diode (IRED) was affixed to the nail of the right index finger and its spatial position was sampled at 200 Hz for 1.5 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 and Statistical Analyses

The angle between the target stimulus and ultimate movement endpoint was determined for each trial. We used standard circular statistics techniques (Batschelet, 1981) via the CircStat Toolbox (Berens, 2009) for MATLAB to calculate

FIGURE 3. Achieved angle (i.e., the angle between the target stimulus and movement endpoint) as a function of the instruction angle for the visuomotor mental rotation (VMR) task. The axis labels are identical for each plot and thus are only shown for the VMR trials in the 30° instruction angle block. The location of the target stimulus has been normalized to 0°. Each data point represents one trial. The large arrow represents the mean direction of all trials. Hatched lines represent one standard deviation (CSD). All units of measure are in degrees.

the mean direction of movement (i.e., the direction of the mean vector) and the associated circular standard deviation (CSD; within-participant standard deviation of movement direction). RT was defined as the time from the color change of the fixation cross to movement onset. In line with our previous work (Neely & Heath, 2010a, 2010b), we evaluated median RT because the distribution of RT was positively skewed.[5] Movement time (MT) was defined as the time from movement onset to movement offset. In most cases (see subsequent exception) dependent variables were submitted to independent 2 Task (standard, VMR) × 7 Instruction Angle (30°, 60°, 90°, 120°, 150°, 180°, 210°) fully repeated measures analyses of variance (ANOVA). Main effects were decomposed via simple effects analyses or power polynomials (Pedhazur, 1997). All statistical tests were evaluated at an alpha level of .05.

Results

Results for mean direction yielded main effects for task, $F(1, 10) > 4500$, instruction angle, $F(6, 60) = 494.80$, ps

$< .001$, and their interaction, $F(6, 60) = 464.57$, $p < .001$. As demonstrated in Figure 2, movement endpoints in the standard task showed directional accuracy that was refractory to the different blocks of instruction angles used here, $F(6, 60) = 1.17$, $p = 0.33$, b $= 0.01°$). In turn, as shown in Figure 3, the VMR task showed a reliable effect of instruction angle, $F(6, 60) = 487.96$, $p < 0.001$, that was best described by a first-order polynomial, $F(1, 10) > 9000, p < .001$, b $= 0.99°$); that is, participants scaled the direction of their reach as per the task instruction. Interestingly, examination of Figure 3 shows that the perceptually familiar angles of 90° and 180° were associated with enhanced directional accuracy relative to perceptually less familiar angles (i.e., 30°, 60°, 120°, 150°, and 210°).

The results for RT and CSD yielded significant main effects of task, for RT, $F(1, 10) = 151.87$, for CSD, $F(1, 10) = 218.77$, ps $< .001$; instruction angle, for RT, $F(6, 60) = 25.16$, for CSD, $F(6, 60) = 8.60$, ps $< .001$; and their interaction, for RT, $F(6, 60) = 22.48$, for CSD, $F(6, 60) = 8.51$, ps $< .001$. For each instruction angle block, the standard task exhibited RT and CSD values that were shorter and more stable,

TABLE 1. Planned Comparisons Between the Standard and VMR Tasks at Each Level of the Independent Variable

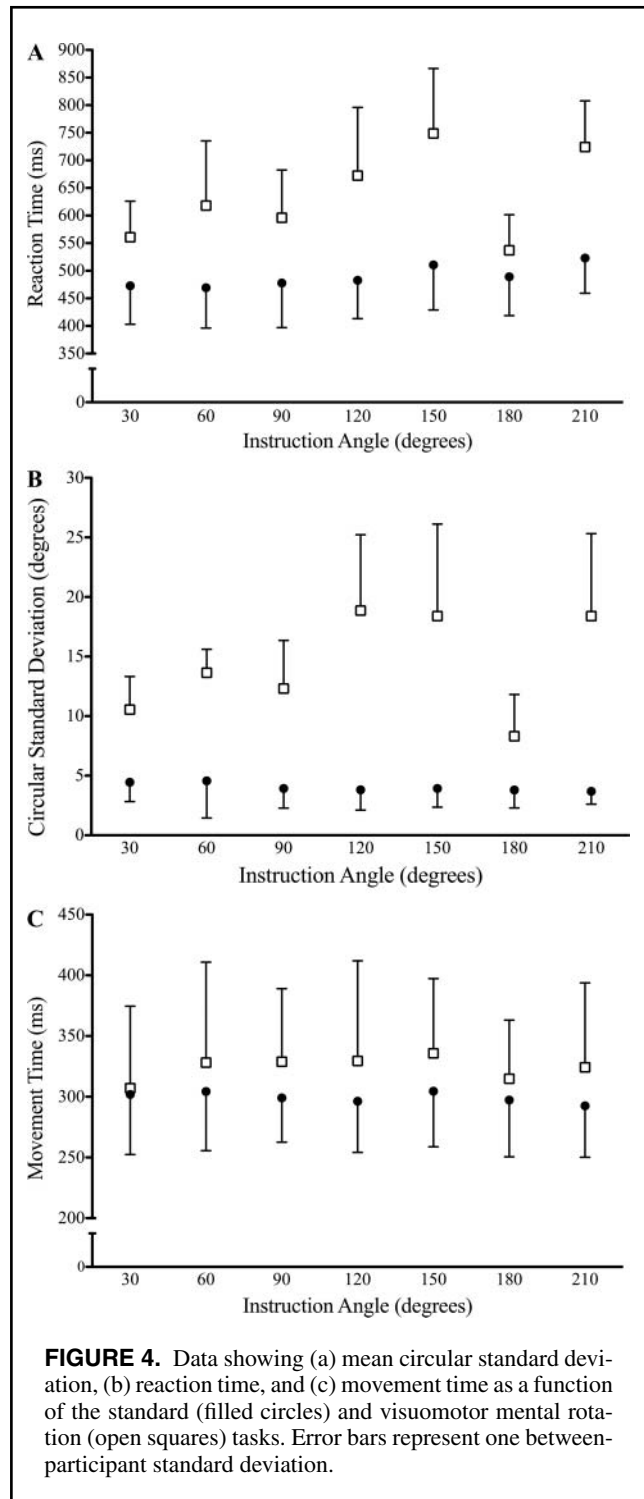|	Measure	
Task	RT	CSD
30°: Standard vs. VMR	−5.54	−8.24
60°: Standard vs. VMR	−6.85	−7.45
90°: Standard vs. VMR	−8.87	−6.71
120°: Standard vs. VMR	−8.19	−8.42
150°: Standard vs. VMR	−11.38	−6.08
180°: Standard vs. VMR	−6.17	−5.88
210°: Standard vs. VMR	−12.08	−7.40

Note. For all comparisons, $p < .001$. RT and CSD data are *t* statistics ($df = 10$). RT = reaction time; CSD = circular standard deviation.

respectively, than counterpart VMR tasks (all $ps < .001$: for post hoc contrasts see Table 1). In addition, Figure 4 shows that the RT and CSD values associated with the standard task were not differentially influenced by the instruction angle block ($ps > .05$), whereas trials associated with the VMR task were differentially influenced by the instruction angle ($ps < .01$). To further address this interaction, we computed between-task difference scores (VMR and standard trials) for each instruction angle. The benefit of this decomposition technique is that the comparable between-task visuomotor inhibition used in our design provides a direct means to examine the movement planning (i.e., RT) and control (i.e., CSD) costs related to the VMR task. Between-task difference scores for RT and CSD were submitted to separate one-way (instruction angle: 30°, 60°, 90°, 120°, 150°, 180°, 210°) repeated measures ANOVAs. Results yielded an effect of instruction angle for each dependent variable, for RT, $F(6, 60) = 22.48$, for CSD, $F(6, 60) = 8.51$, $ps < .01$, such that RT and instruction angle as well as CSD and instruction angle were best described by a fifth-order polynomial, for RT, $F(1,10) = 47.93$, for CSD, $F(1,10) = 54.03$, $ps < .001$. We interpret this complex relationship as evidence for reduced temporal demands for the planning and control of standard and VMR responses when the visuomotor transformations are small (30°) or perceptually familiar (90° and 180°). Moreover, Figure 5 demonstrates that RT and CSD values did not increase linearly with increasing instruction angle.
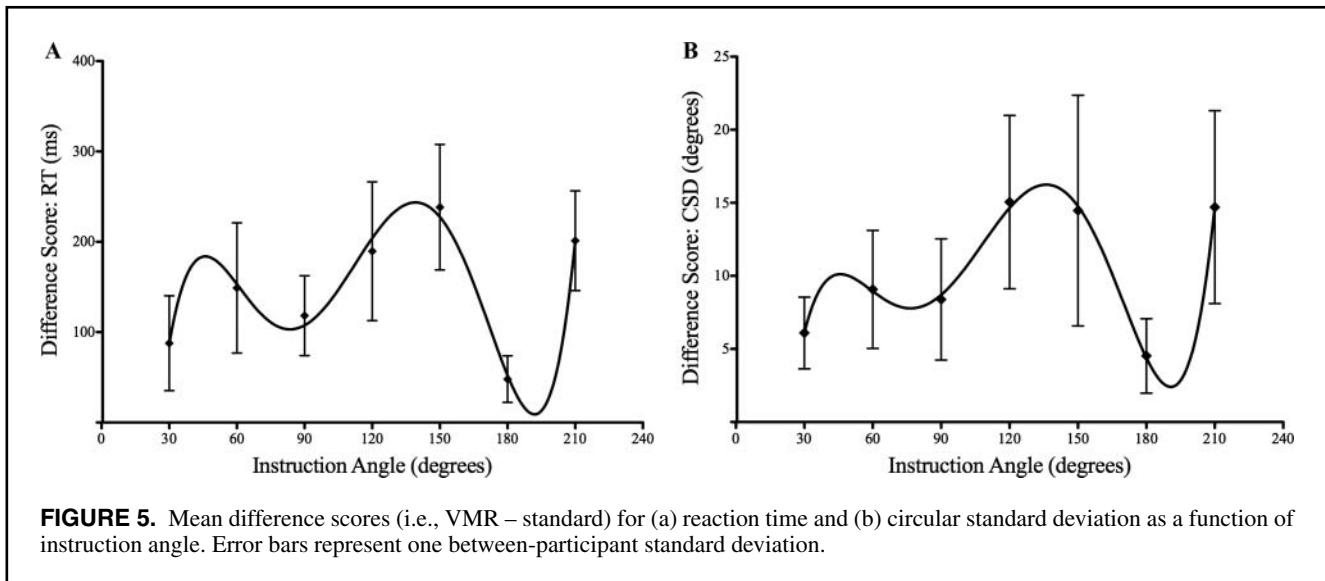
The results for MT revealed an effect of task, $F(1, 10) = 11.04$, $p < .01$, such that trials in the standard task produced shorter movement durations ($M = 300$ ms, $SD = 43$ ms) than their VMR counterparts ($M = 324$ ms, $SD = 66$ ms).

Discussion

The goal of this study was to isolate the time cost of visuomotor transformations in the VMR task. We used a randomized task design to determine the magnitude of the RT

FIGURE 4. Data showing (a) mean circular standard deviation, (b) reaction time, and (c) movement time as a function of the standard (filled circles) and visuomotor mental rotation (open squares) tasks. Error bars represent one between-participant standard deviation.

difference between standard and VMR tasks across a range of angles: 30°, 60°, 90°, 120°, 150°, 180°, and 210°. The present results demonstrate that visuomotor transformations are more efficient and effective when the response entails a degree of dimensional overlap between target and response (i.e., when the angular disparity between the responses is small) or when the transformation angle is perceptually

FIGURE 5. Mean difference scores (i.e., VMR – standard) for (a) reaction time and (b) circular standard deviation as a function of instruction angle. Error bars represent one between-participant standard deviation.

familiar. Qualitative comparison between Figure 4 of the present study and Figure 3 of our previous work (Neely & Heath, 2010a) demonstrates parallel results for RT. More important, the present study extends our previous work (Neely & Heath, 2009, 2010a, 2010b) by demonstrating that between-task differences in RT are attributed to the temporal demands of visuomotor transformations and not to the temporal demands of response inhibition.

Endpoints for the Standard and the VMR Tasks Adhere to Response Instructions

The first issue is whether participants demonstrated a level of directional accuracy congruent with task instructions. Figure 2 shows that endpoints for the standard task were refractory to the block in which they were performed. That is, the possibility of completing a 30° VMR response (or any other angle) did not influence the direction (i.e., MD) or distribution (i.e., CSD) of standard task endpoints. This finding is in accord with work showing that actions with spatial overlap between a target and a response are mediated via dedicated visuomotor networks that operate independent of the context-dependent properties of the reaching environment (e.g., Goodale et al., 1986). In the VMR task, endpoints scaled to instruction angle, demonstrating that the motor system provides the requisite spatial resolution to support the transformation angles studied here. However, and as shown in Figure 3, transformations of 90° and 180° were more accurate and less variable than the other angles. We recognize that a potential reason for this improved performance is use of four target locations equally divided by 90°. This target arrangement may have enabled participants to develop a more stable visuomotor representation of those locations in space by virtue of the fact that participants pointed to these locations more often than other locations in the reaching area. Although

this is a potential limitation of the present work, it is important to note that this finding is consistent with work from the perceptual literature demonstrating that judgments related to right angles and straight lines elicit greater perceptual stability than those related to acute and obtuse angles (e.g., McFarland, 1968; see also Howe & Purves, 2005; Nundy et al., 2000). Moreover, this finding supports the assertion that the top-down and cognitive nature of the VMR task renders motor output that is supported by a perceptual representation of visual space (Heath, Maraj, Gradkowski, et al., 2009; Heath, Maraj, Maddigan, et al., 2009; Maraj & Heath, 2010). In particular, previous work examining the antipointing task demonstrates that movement endpoints yield a visual-field specific pattern of endpoint bias such that responses in the left visual field undershot veridical target location, whereas responses in the right visual field overshot veridical target location. This pattern of endpoint bias is consistent with results from the perceptual literature demonstrating that obligatory judgments of target extent are over- and underestimated in the left and right visual fields, respectively (Charles, Sahraie, & McGeorge, 2007).

The Extent and Familiarity of VMR Transformation Angles Influence RTs

RTs for the standard task were shorter than those for the VMR task across each of the transformation angles investigated here. Moreover, the standard task yielded shorter MTs and more stable endpoints than counterpart VMR trials. In keeping with the preceding section, such a pattern of results demonstrates that actions with spatial overlap between target and response are supported by fast, stimulus-driven visuomotor networks that optimize the efficiency and effectiveness of motor output (e.g., Neely & Heath, 2009, 2010a).[6] In contrast, the longer RTs and MTs, and more variable movement

endpoints of the VMR task indicates that actions involving a spatial dissociation between target and response are mediated via a slow mode of cognitive mode of control that is not optimized to support motor output (Heath, Maraj, Gradkowski, et al., 2009; Heath, Maraj, Maddigan, et al., 2009; see also Rossetti et al., 2005).

However, of greater interest to the present investigation was to quantify how different instruction angles influence the speed of visuomotor transformations. To this end, we randomly interleaved standard and VMR tasks to equate between-task response inhibition and then computed difference scores (VMR task – standard task) to index the cost of angle-specific visuomotor transformations. RT differences were least for small (i.e., 30°) and perceptually familiar (i.e., 90° and 180°) angles in comparison with large and less familiar angles (i.e., 60°, 120°, 150°, and 210°). This finding counters the tenets of the mental rotation model, which asserts that RT increases as a function of increasing instruction angle, for all angles up to and beyond 180° (Georgopoulos & Massey, 1987). Instead, the present results are in accord with a process of response substitution and the contention that spatial (i.e., angular disparity) as well as cognitive (i.e., perceptual expertise) factors influence the speed of visuomotor transformations. In particular, visuomotor transformations are faster when the response entails a degree of dimensional overlap between target and response (i.e., when the angular disparity between the responses is small) or when the transformation angle is perceptually familiar.

The literature examining the two-target task provides a framework for understanding how spatial and cognitive factors impact the response substitution process. In this task, participants are presented with two visual targets and after a variable delay, one of the targets is identified as the response goal. Electrophysiological studies show that mutually exclusive peaks of neural activity simultaneously develop when the two targets are disparate from one another; however, when movement outcomes are closer together, targets are represented via a continuous plateau of activation (Bastian, Schoner, & Riehle, 2003; Cisek & Kalaska, 2005). Thus, the response substitution process and consequent behavioral RTs are shorter when the distance between potential movements is reduced relative to when they are far apart (Bock & Eversheim, 2000; Favilla, 2002; Praamstra, Kourtis, & Nazarpour, 2009). We recognize that the salient difference between the two-target task and the present study is that the VMR task requires the second target to be represented conceptually as opposed to veridically. Given this difference, we suggest that the onset of the visual target in our task elicits an initial burst of neural activity reflecting a planned response to the target. This response is inhibited until the task instruction (standard or VMR) is delivered. If a transformation is required, another burst of neural activity develops to reflect the location of the VMR response. If the transformation angle is small (e.g., 30°), the two peaks of neural activity overlap and a shorter RT is observed. In contrast, if the transformation angle is large (e.g., 120°), motor planning areas have to select the appropriate response from two discrete neural correlates, thereby resulting in a longer RT.

The second notable element of this work is the demonstration that visuomotor transformations of 90° and 180° elicit more effective and efficient motor output relative to transformations involving acute and obtuse angles. We propose that such a pattern of results is the consequence of enhanced perceptual stability for angles of 90° and 180°. Work from the perceptual literature reports superior visual discrimination for stimuli appearing at cardinal orientations in comparison to those that appear at oblique orientations (e.g., the oblique effect; Jastrow, 1893; for a review see Appelle, 1972). Further, McFarland (1968) demonstrated enhanced perceptual stability for right angles and straight lines compared with acute and obtuse angles. Thus, the present study suggests a response substitution process influenced by an individual's perceptual familiarity with the required angle of rotation. In other words, perceptual familiarity related to a desired movement outcome influences the rate of response substitution.

The affordance competition hypothesis (Cisek, 2006, 2007) provides a framework for understanding how neurophysiological and cognitive factors could influence the response substitution process. Specifically, a frontoparietal network specifies multiple potential actions that compete against one another for response selection. In accord with the literature describing the two-target task (Bastian et al., 2003; Cisek & Kalaska, 2005), these actions are represented as multiple distributions of neural activation in motor planning areas. Other brain areas, such as the prefrontal cortex (Hoshi, Shima, & Tanji, 2000) and the basal ganglia (Redgrave, Prescott, & Gurney, 1999), continuously accumulate sensory evidence for each alternative while the frontoparietal network determines which action is most appropriate. When sufficient evidence is available in favor of one of the response alternatives, the distribution representing the opposing response decays and the selected action is initiated. Importantly, the affordance competition hypothesis explicitly predicts that RTs are reduced when potential movement outcomes are in close spatial proximity to one another. As the VMR task represents a corollary to the two-target task, the tenets of the affordance competition hypothesis are in accord with the present finding that response preparation is faster when the angular disparity between response alternatives is small relative to when the disparity is large. Moreover, the model's assertion of an integrated system of perception, action, and cognition provides a mechanistic framework for understanding the influence of perceptual expertise on the parameters of the VMR response.

Conclusions

The goal of this study was to isolate the time cost of visuomotor transformations in the VMR task. The results demonstrated that visuomotor transformations are more efficient and effective when the response entails a degree of dimensional overlap between target and response (i.e., when

the angular disparity between the responses is small) or when the transformation angle is perceptually familiar. This finding counters the tenets of the mental rotation model (Georgopoulos & Massey, 1987), but is in accord with a process of response substitution wherein spatial (i.e., angular disparity) and cognitive (i.e., perceptual expertise) factors influence the speed of visuomotor transformations.

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NOTES

1. Our use of the term *dimensional overlap* is consistent with the stimulus-response compatibility literature describing degrees of commonality or similarity between a stimulus and a response (Kornblum, Hasbroucq, & Osman, 1990). In terms of the present work, such commonality is determined by the spatial disparity between the stimulus-driven and the VMR responses.

2. Although some VMR studies have examined eye movements (de'Sperati, 1999; Fischer, Deubel, Wohlschlager, & Schneider, 1999), our discussion of the VMR literature is restricted to limb movements.

3. There is no evidence from Georgopoulos and Massey (1987) to suggest the mental rotation model (MRM) predicts RT only for the set of angles used in their manuscript. Moreover, it is important to note that exemplar neurophysiological evidence describes mental rotation of the neuronal population vector for $90°$ (see Figure 1 of Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989).

4. On average, participants reported one directional error per block of trials. Some participants completed several blocks in a row without making an error. To determine (offline) if participants initially specified their reach trajectory in line with the task instructions, we calculated mean direction at peak acceleration. The results of this analysis were consistent with the results for mean direction at ultimate movement endpoint. For the standard trials, there was no effect of instruction angle, $F(6, 60) = 1.07$, $p = .392$. Specifically, mean direction was in line with the veridical target coordinates. For the VMR trials, the F statistic demonstrated an effect of instruction angle, $F(6, 60) = 257.93$, $p < .001$, such that the direction of the reach trajectory increased as a function of increasing instruction angle. Post hoc analysis demonstrated that mean direction was different for each instruction angle (all $ps < .003$).

5. To determine whether RT was normally distributed, we examined the ratio of the skewness value to its associated standard error. The skewness statistic was 17.73 and thus we elected to evaluate the medians.

6. The reference in the preceding cited literature focus on spatial data, whereas the examples cited focus on temporal data.

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