BRAIN RESEARCH

Research Report

Visuomotor mental rotation: Reaction time is determined by the complexity of the sensorimotor transformations mediating the response

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ABSTRACT

In the visuomotor mental rotation (VMR) task, participants point to a location that deviates from a visual target by a predetermined angle. A seminal investigation of the VMR task reported a linear increase in reaction time (RT) as a function of increasing angle, for 5°, 10°, 15°, 35°, 70°, 105°, and 140° (Georgopoulos and Massey, 1987). This finding led to the development of the mental rotation model (MRM) and the assertion that response preparation is mediated via the imagined rotation of a movement vector. To determine if the MRM can be extrapolated to perceptually familiar angles (e.g., 90° and 180°) within a range of equally spaced angles, we evaluated two independent sets of angles: 5°, 10°, 15°, 35°, 70°, 105°, and 140° (experiment one) and 30°, 60°, 90°, 120°, 150°, 180°, and 210° (experiment two). Consistent with the MRM, experiment one revealed a linear increase in RT as a function of increasing angle; however, a non-linear relation was revealed for experiment two. RTs were fastest for 180°, followed by 30°, 90°, 60°, 150°, 210°, and 120°. Such results demonstrate that response preparation was not uniquely mediated via a mental rotation process. Instead, the present work provides evidence of a temporally demanding and cognitively mediated response substitution process, wherein the computational demands of response preparation are determined by the complexity of the sensorimotor transformations mediating the response.

1. Introduction

In the visuomotor mental rotation (VMR) task—a motor variant of the classic mental rotation task (e.g., Shepard and Metzler, 1971)—participants execute a center-out reaching movement to a location that deviates from a visual target by a predetermined angle (Georgopoulos and Massey, 1987). Behavioral investigations of the VMR task report a linear increase in reaction time (RT) as a function of increasing instruction angle, for 5°, 10°, 15°, 35°, 70°, 105°, and 140° (Georgopoulos and Massey, 1987; Pellizzer and Georgopoulos, 1993; for a review, see Georgopoulos and Pellizzer, 1995). This finding led to the mental rotation model (MRM) and the assertion that response

preparation is mediated via the imagined rotation of a movement vector (Georgopoulos and Massey, 1987). Further support for the MRM was garnered from single-cell recording studies that report a gradual shift of neural activation during the response preparation phase of the task (Georgopoulos et al., 1989; Lurito et al., 1991). Specifically, the weighted vector sum of neural activity (i.e., the population vector) in motor cortex initially reflects the location of the visual target; however, over time, the population vector rotates to reflect the direction of the to-be-completed motor response (Georgopoulos et al., 1989; Lurito et al., 1991). Importantly, the MRM describes an analog process wherein intermediary angles are represented by shifting populations of neurons in cortical motor areas.

In contrast to the work of Georgopoulos et al. (1989; Lurito et al., 1991), Cisek and Scott's (1999) response substitution hypothesis (RSH) asserts that the VMR task elicits two distinct neural representations, one representing the visual target and another representing the direction of the appropriate motor response. Through a process of response substitution, the activity representing the stimulus decays while that representing the to-be-completed motor response increases to threshold for movement initiation. Importantly, the RSH asserts that RTs reflect the rate of this process. The time to reach threshold for movement initiation is optimized when the visual target and movement outcome are spatially aligned (Cisek and Scott, 1999). This relationship is the consequence of a larger, continuous plateau of neural activation that develops when potential movement outcomes are close together. In contrast, mutually exclusive and discrete peaks of activation develop as the angular disparity between the visual target and motor outcome increases. Response preparation is fastest when the distribution characterizes both the direction of the visual target and the movement outcome (i.e., small transformation angles) and increases systematically as the distributions become more disparate. Notably, subsequent multi-target studies report faster RTs when the distance between multiple potential movements is reduced relative to when they are far apart (Bock and Eversheim, 2000; Favilla, 2002; Praamstra et al., 2009).

The aforementioned work from Georgopoulos et al. (1989; Georgopoulos and Massey, 1987; Lurito et al., 1991) and Cisek and Scott (1999) is consistent with the idea that tasks entailing spatial overlap between a visual stimulus and a motor response (so-called standard mapping) allow for motor output to be supported by maximally efficient and effective stimulus-driven visuomotor networks (Fitts and Seeger 1953; Kornblum et al., 1990). In contrast, when a visual stimulus and the movement goal are not spatially aligned (so-called nonstandard mapping), a stimulus-driven response must be suppressed via top-down executive control and the appropriate angular difference between stimulus and response must be computed in advance of movement onset. In particular, behavioral investigations show that the antipointing task, a VMR task requiring a transformation of 180°, is mediated via cognitive control—a mode of control that operates on a slower time scale than stimulus-driven visuomotor networks (Heath et al., 2009a, 2009b; Maraj and Heath, 2010). The basis for this finding stems from work demonstrating that antipointing elicits slower response

latencies than a standard mapping task, as well as a visual field specific endpoint bias commensurate with the well-documented perceptual over- and underestimation of object properties in a left and right space, respectively (Charles et al., 2007; Elias et al., 2002; Heath et al., 2009a, 2009b; Luh et al., 1995; Nicholls et al., 1999). In line with this work, we recently reported that perceptual expertise influences response latencies in VMR tasks requiring transformations of 90° and 180° (Neely and Heath, 2009, 2010). Specifically, a response planning advantage emerged when a visual target and subsequent motor response were congruent with the cardinal axes. In addition, we revealed an RT advantage for sensorimotor transformations of 180° relative to 90°, regardless of whether the visual stimulus (and thus motor output) was congruent or incongruent with the cardinal axes and regardless of whether the response was performed with the left or right hand (Neely and Heath, 2009, 2010). Notably, these results are counter to the MRM; that is, if mental rotation of an imagined movement vector had mediated response planning, then RTs for 90° would have been faster than those for 180°. Instead, we argued that the results were an evidence of a process of response substitution influenced by the computational demands of the sensorimotor transformations mediating the VMR response. Specifically, we suggested that transformations of 180° are computationally less demanding (than those required for transformations of 5°, 10°, 15°, 35°, 70°, 105°, and 140°) and thus lead to an enhanced rate of response substitution in the VMR task. Without intermediate angles, however, we were unable to determine whether the increased RTs for 90° were evidence of a mental rotation (or any other) strategy.

The present work was designed to provide a test of the MRM by examining 90° and 180° in concert with perceptually unfamiliar angles. In experiment one, we conducted a reevaluation of the angles used by Georgopoulos and Massey (1987; i.e., 0°, 5°, 10°, 15°, 35°, 70°, 105°, and 140°). In experiment two, we examined a set of equally spaced angles (i.e., 0°, 30°, 60°, 90°, 120°, 150°, 180°, and 210°), which included the perceptually familiar angles of 90° and 180°. Notably, both the MRM and the RSH predict that response latencies are influenced by the angular disparity between the target and the motor outcome. However, due to the analog nature of mental rotation, a strict interpretation of the MRM predicts a linear relation between RT and instruction angle, for all angles up to and beyond 180° (e.g., Georgopoulos and Massey, 1987). Moreover, the MRM does not include a provision to suggest that the rate of rotation is subject to cognitive (or any) influence. In contrast, the RSH posits that RTs reflect the time cost of the response substitution process. Although the temporal duration of this process is, in part, determined by the angular disparity between the target and the motor outcome, we assert that the RSH provides flexibility to account for other factors that may influence the rate of this process. In particular, we hypothesize that the rate of response substitution is influenced by perceptual expertise with the transformation angle. Specifically, the visual system's enhanced discrimination of right angles and straight lines (Jastrow, 1893; Howe and Purves 2005; McFarland, 1968; Nundy et al. 2000; for a review, see Appelle, 1972) differentially influences
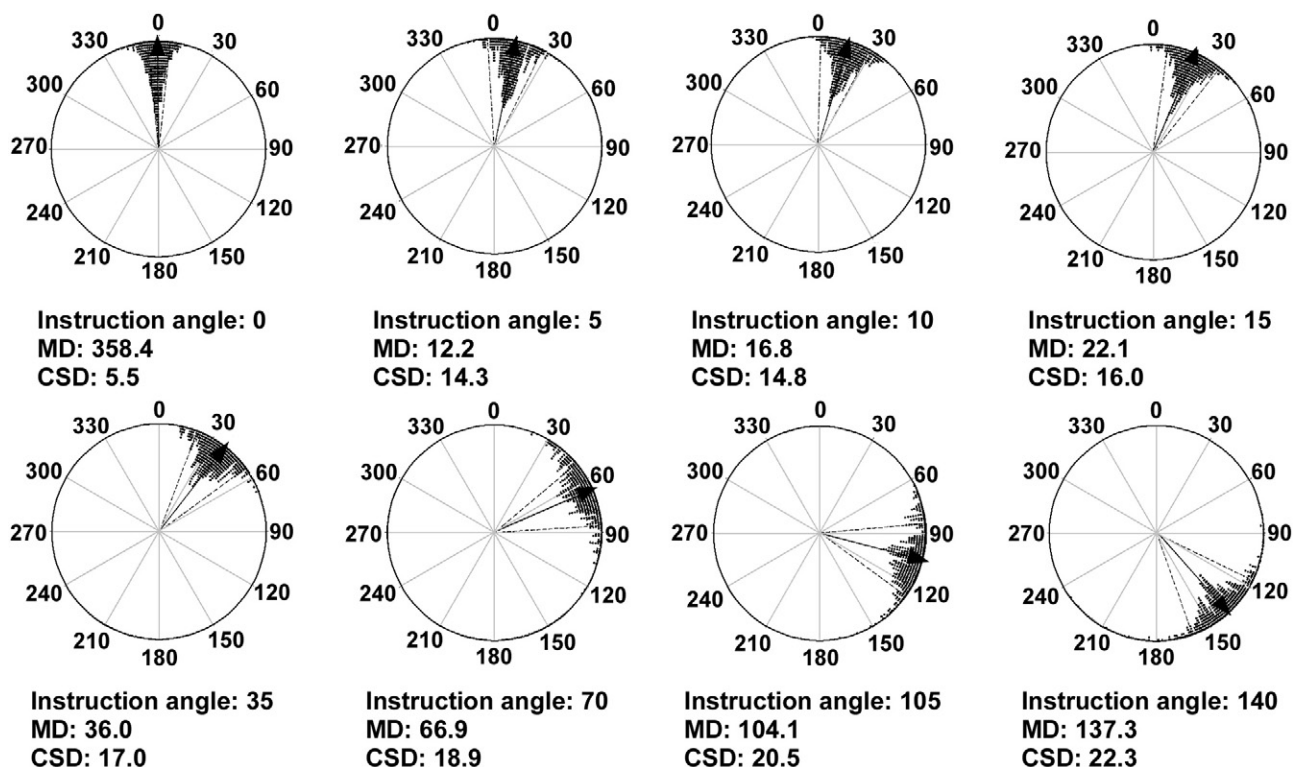
Fig. 1 – Achieved angle (i.e., the angle between the target stimulus and movement endpoint) as a function of instruction angle for experiment one. Each data point represents one trial. The location of the target stimulus has been normalized to 0°. The large arrow represents the mean direction (MD) of all trials. Hatched lines represent one standard deviation (CSD). All units of measure are in degrees.

the speed and effectiveness of visuomotor transformations of 90° and 180°.

2.   Results

The angle of rotation achieved on a trial-by-trial basis was determined by calculating the angle between the target stimulus and the ultimate movement endpoint, henceforth referred to as the mean direction. In particular, the mean direction describes the angle between the visual target, the starting position of the limb, and movement endpoint. For example, a mean direction of 358° indicates that reaches were directed 2° counterclockwise to the visual target, whereas a mean direction of 38° indicates that reaches were directed 38° clockwise from the visual target. In addition, we computed the within-participant variability of movement direction (the standard deviation associated with the mean direction; degrees). Both mean direction and circular standard deviation were calculated using standard circular statistics techniques (Batschelet, 1981) via the CircStat Toolbox (Berens, 2009) for MATLAB. RT (milliseconds) was defined as the time from the onset of the target stimulus to movement onset. We evaluated median RT and its associated measure of variability (i.e., semi-interquartile range, henceforth referred to as variable reaction time, VRT;

milliseconds) because the distribution of RT in experiments one and two was positively skewed.[1] Movement time (milliseconds) was computed as the time from movement onset to movement offset.

In most cases (exceptions are noted below), dependent variables were submitted to independent one-way (instruction angle: 0°, 5°, 10°, 15°, 35°, 70°, 105°, and 140° [experiment one] or 0°, 30°, 60°, 90°, 120°, 150°, 180°, and 210° [experiment two]) fully repeated measures analyses of variance (ANOVA) and main effects were decomposed via simple effects and/or power polynomials (Pedhazur, 1997). Importantly, to appropriately fit polynomials to main effects, we adopted a standard orthogonalization procedure (Monlezun, 1999; see also Carmer and Seifm, 1963) for experiment one because consecutive levels of the independent variable (i.e., instruction angle) were not equally spaced. In particular, the main effect sums of squares were partitioned into individual, one-degree

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[1] In order to determine whether RT was normally distributed, we examined the ratio of the skewness value to its associated standard error. Skewness statistics for experiments one and two were 23.41 and 13.77, respectively. We thus elected to evaluate median RT and its associated measure of variability (i.e., semi-interquartile range).
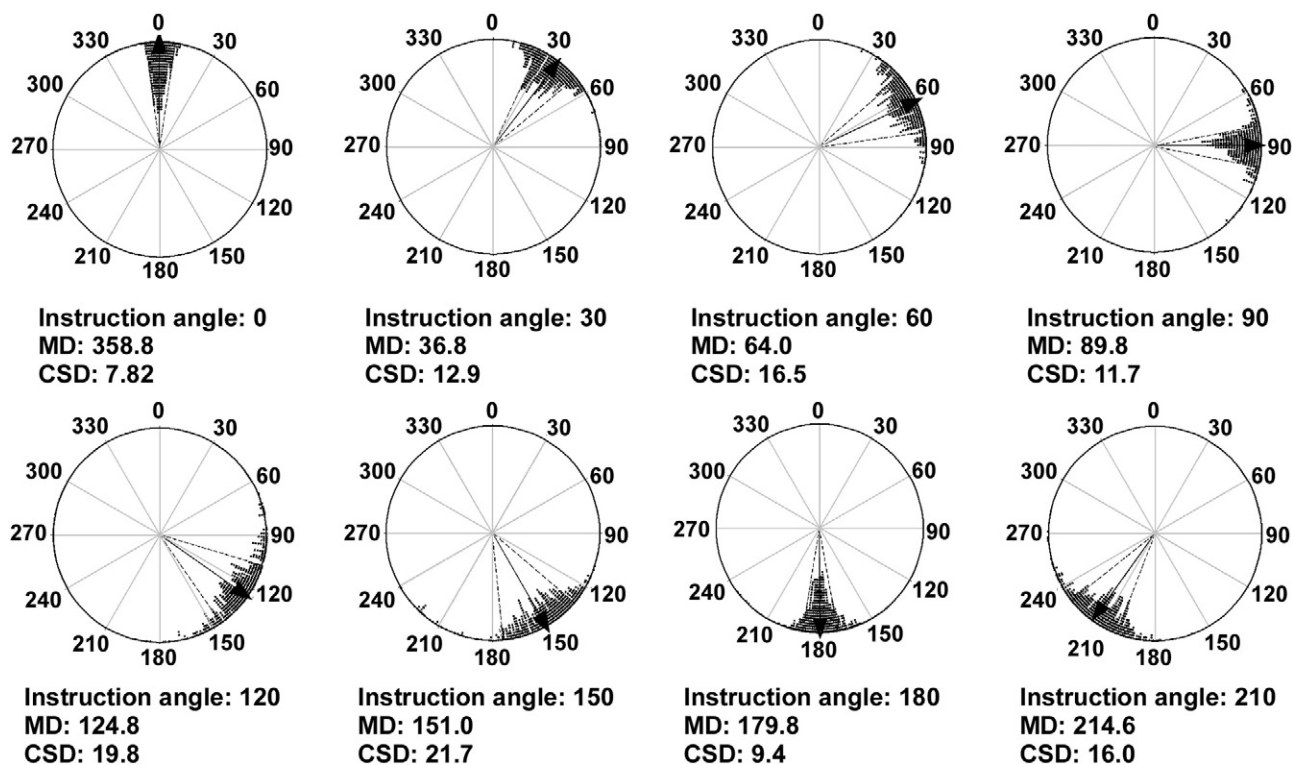
Fig. 2 – Achieved angle (i.e., the angle between the target stimulus and movement endpoint) as a function of instruction angle for experiment two. Conventions are as described in Fig. 1.

of freedom sums of squares for tests of significance of the polynomial coefficients.

2.1.   Direction of movement

It is important to demonstrate that participants adhered to the task instructions and performed an appropriate VMR response to each instruction angle. Figs. 1 and 2 present trial-to-trial achieved angle data for all participants as a function of each instruction angle. As shown in these figures, mean direction scaled to instruction angle, $Fs(6,54) = 749.59$ and 839.14, respectively, for experiments one and two, $ps < .001$, all pairwise comparisons, $ps < .05$. Not surprisingly, mean direction for the standard mapping task (i.e., the 0° instruction angle) was more commensurate with veridical endpoint location than any of the VMR tasks used here.

2.2.   Stimulus-driven versus voluntary responses

To confirm that latencies for the standard mapping task were faster than any of the instruction angles associated with the VMR task, we conducted *a posteriori* contrasts between RT for the 0° instruction angle with the VMR task producing the fastest RT. For experiment one, RT for the 0° instruction angle (397 ms SD 49) was faster than the 5° instruction angle (474 ms SD 54; $t(9) = -5.59$, $p < .001$; see Fig. 3). For experiment two, the 0° instruction angle (376 ms SD 61) was faster than the 180° instruction angle (451 ms SD 74; $t(9) = --10.46$, $p < .001$; see Fig. 3).

2.3.   Response parameters of the VMR task

The primary goal was to evaluate the response parameters associated with different instruction angles for a VMR task. Thus, we did not include the 0° instruction angle in subsequent analyses. The analyses of RT, VRT, circular standard deviation, and movement time for the VMR trials yielded a reliable effect of instruction angle across each dependent variable and for each experiment (see Table 1 for ANOVA summary table). Notably, the examination of RT for experiment one indicated a linear increase in RT as a function of increasing instruction angle (see Fig. 3). Moreover, the examination of the other dependent variables elicited a similar effect, that is, VRT, circular standard deviation, and movement time increased in relation to increasing instruction angle (Fig. 4). In contrast, the RT findings for experiment two were non-linear and the data were best described by a fifth-order polynomial (see Fig. 3).[2] Although we recognize that the interpretation of a fifth-order polynomial is not a parsimonious one, this finding indicates that RTs did not

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[2] Importantly, the removal of perceptually familiar angles (i.e., 90° and 180°) does not result in a linear trend for the remaining instruction angles (highest-order polynomial: fourth-order, $F(1,9) = 7.04$, p = .026).
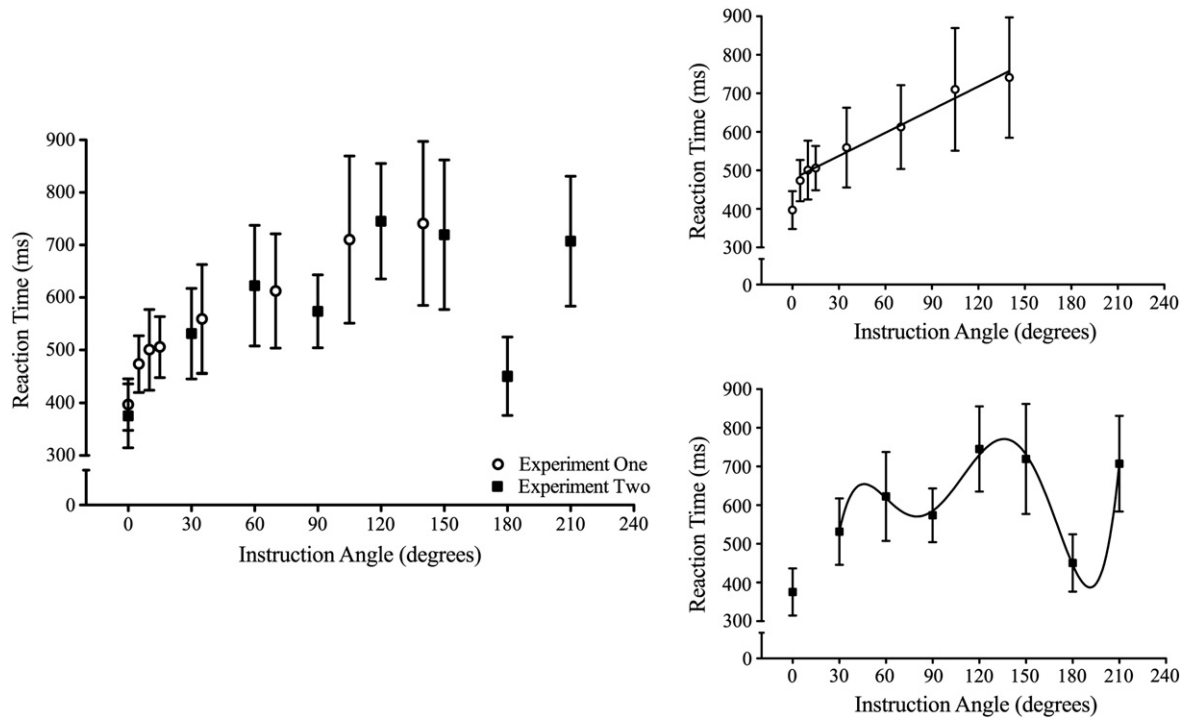
Fig. 3 – Mean RT as a function of instruction angle, for experiments one and two (left panel). The results for experiment one (top right panel) reveal a linear relationship between RT and instruction angle. In contrast, the results for experiment two (bottom right panel) demonstrate that the relationship between RT and instruction angle is best described by a fifth-order polynomial. Error bars reflect one between-participant standard deviation.

scale to instruction angle as predicted by the MRM. The findings for VRT, circular standard deviation, and movement time were consistent with the RT findings, that is, the relationship between each dependent variable and instruction angle was best described by a fifth-order polynomial (see Fig. 4).

3. Discussion

Seminal investigations of the VMR task report a linear increase in RT as a function of increasing angle (Georgopoulos and Massey, 1987). Such results led to the development of the MRM and the assertion that response latencies reflect the time required for the imagined rotation of a movement vector (Georgopoulos and Massey, 1987). In contrast, we recently reported a response planning advantage for transformations of 180° relative to 90° (Neely and Heath, 2009, 2010). Furthermore, we demonstrated that this phenomenon was not limited to situations wherein the visual stimulus and motor output were congruent with the cardinal axes (Neely and Heath, 2010). We interpreted these findings as evidence that visuomotor transformations of 180° are mediated by a computationally less demanding response substitution process, whereas all other angles may evoke a mental rotation strategy. Without having tested intermediate angles, however, we were unable to determine if this was the case. Thus, the goal of the present work was to provide a critical test of the MRM by examining the response parameters of a VMR task across a series of equally spaced angles, which included the perceptually familiar angles of 90° and 180°.

Table 1 – The results of the one-way (instruction angles: 5°, 10°, 15°, 35°, 70°, 105°, and 140° [experiment one] and 30°, 60°, 90°, 120°, 150°, 180°, and 210° [experiment two]) fully repeated measures ANOVA. The first row (under each dependent variable) represents the Omnibus F and the second row presents the highest-order polynomial. p-values less than .001 are denoted by double asterisks (**); p-values less than .05 are denoted by a single asterisk (*).

Dependent variable	Experiment	
	Experiment one	Experiment two
RT		
	$F_{(6,54)} = 20.93^{**}$	$F_{(6,54)} = 40.95^{**}$
	Linear: $F_{(1,9)} = 41.16^{**}$	Fifth-order: $F_{(1,9)} = 62.86^{**}$
VRT		
	$F_{(6,54)} = 7.82^{**}$	$F_{(6,54)} = 10.26^{**}$
	Linear: $F_{(1,9)} = 19.61^{*}$	Fifth-order: $F_{(1,9)} = 34.11^{**}$
MT		
	$F_{(6,54)} = 3.96^{*}$	$F_{(6,54)} = 3.74^{*}$
	Linear: $F_{(1,9)} = 13.83^{*}$	Fifth-order: $F_{(1,9)} = 6.23^{*}$
CSD		
	$F_{(6,54)} = 29.62^{**}$	$F_{(6,54)} = 10.34^{**}$
	Linear: $F_{(1,9)} = 55.76^{**}$	Fifth-order: $F_{(1,9)} = 26.18^{*}$

Note. RT = reaction time, VRT = variable reaction time, MT = movement time, and CSD = circular standard deviation.
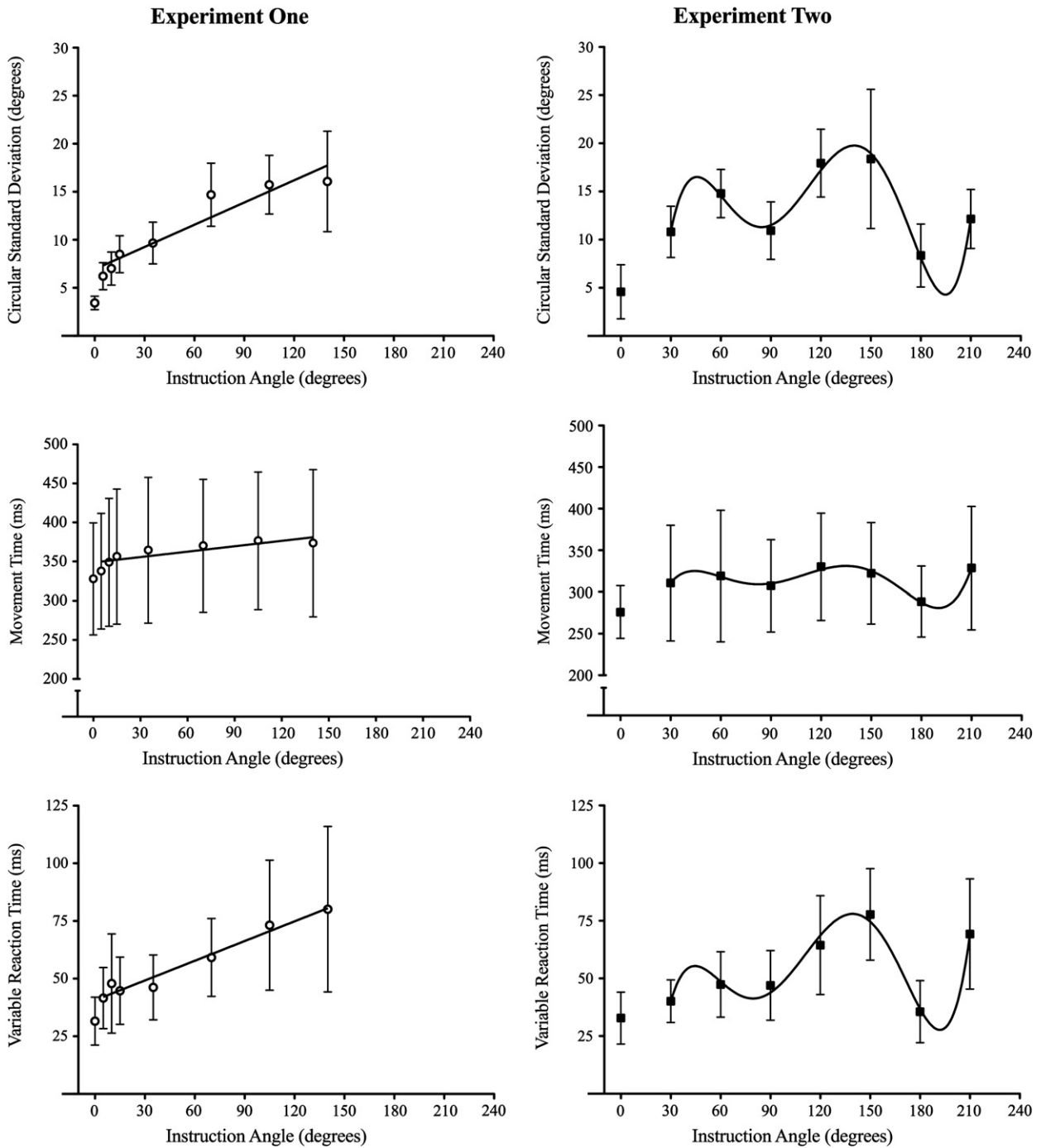
Experiment One

Experiment Two

Fig. 4 – Mean circular standard deviation (top row), movement time (middle row), and VRT (bottom row) for experiments one (left panel) and two (right panel). The data from experiment one reveal a linear relationship between each dependent variable and instruction angle. In contrast, the data from experiment two demonstrate that the relationship between each dependent variable and instruction angle is best described by a fifth-order polynomial. Error bars reflect one between-participant standard deviation.

3.1. Stimulus-driven actions optimize the effectiveness and efficiency of motor output

The first issue we address is whether the direction of participant's movement endpoints was congruent with task instructions. The mean direction of participant's endpoints and the associated variability were optimized in the standard mapping condition, an expected finding given this condition provided the highest degree of dimensional overlap between the target stimulus and motor

response.[3] In turn, mean movement direction for transformations of 90° and 180° was more commensurate with instruction angle and elicited greater directional stability than the other VMR angles investigated here. We interpret such results as evidence that perceptual expertise with 90° and 180° serves to optimize the spatial resolution of the VMR response. This assertion is consistent with work from the perceptual literature demonstrating that stability for right angles and straight lines is enhanced relative to acute and obtuse angles (McFarland, 1968). Last, it is important to emphasize that Figs. 1 and 2 demonstrate that participants completed visuomotor transformations in line with the task demands for all remaining angles (i.e., 5°, 10°, 15°, 35°, 70°, 105°, and 140° for experiment one; 30°, 60°, 120°, 150°, and 210° for experiment two). Such results indicate that the visuomotor system affords the requisite spatial resolution to calibrate motor output even when the task involves a spatial dissociation between a stimulus and a response.

The second issue we address is the RT difference between the standard mapping task and the VMR task. Consistent with the findings for movement direction and stability, the fact that RTs were fastest in the standard task indicates that actions entailing the highest degree of dimensional overlap between stimulus and response are associated with maximal efficiency of motor output. The basis for this performance is thought to be rooted in the fact that standard tasks are supported by stimulus-driven visuomotor networks that are optimized to support metrical motor output (Binsted et al., 2007; Carey et al., 1996; Chua et al., 1992; Heath et al., 2009a, 2009b; Heath et al., 2008; Neely and Heath, 2009, 2010; Pisella et al., 2000; Rossetti et al., 2005; for a review, see Milner and Goodale, 2006). In contrast, RTs for the VMR trials were slower and more variable, suggesting that response preparation was computationally more demanding. In particular, prolonged RTs characterizing tasks involving a spatial dissociation between target and response are proposed to provide evidence of a "slow" mode of cognitive control (Heath et al., 2009a, 2009b; Maraj and Heath, 2010; Munoz and Everling, 2004; Neely and Heath, 2009, 2010; see also Rossetti et al., 2005). Indeed, neuroimaging work has demonstrated that the same neural circuits are activated in standard and nonstandard tasks; however, nonstandard tasks involve the recruitment of additional resources within a distributed fronto-parietal network (Connolly et al., 2000, 2002; Curtis and D'Esposito, 2003; Ford et al., 2005). This pattern of increased cortical activation during the premovement period of nonstandard tasks is attributed to increased cognitive control. Moreover, a similar mode of control is hypothesized for sensorimotor adaptation tasks, wherein participants must adapt to altered visual input (e.g., Bock et al., 2001; Held, 1962; Rossetti et al., 1993) or force-field

perturbations (e.g., Shadmehr and Mussa-Ivaldi, 1994). For instance, in the case of altered visual input via prism glasses, the lateral displacement of the visual field necessitates cognitive computations to implement offline corrections to ensuing arm trajectories. Rossetti et al. (1993) have speculated that this increase in RT reflects the use of a cognitive process, such as mental rotation, to mediate such transformations.

3.2. Response preparation is not universally mediated by the imagined rotation of the movement vector

The results for experiment one revealed a linear increase in RT as a function of the increasing instruction angle for 5°, 10°, 15°, 35°, 70°, 105°, and 140°. This represents a faithful replication of the RT results reported by Georgopoulos and Massey (1987). The present investigation required participants to compute the distance and direction parameters of the response "as quickly and accurately as possible" in the absence of visual feedback (see Section 4.3 for details). In addition, we restricted eye movements to prevent oculomotor information from influencing online limb control (e.g., Bock, 1986; Heath, 2005; van Donkelaar, 1997). In contrast, Georgopoulos and Massey (1987) did not provide instructions related to the amplitude or speed of the response. In addition, their work allowed for visual feedback of the limb and target stimulus and did not place restrictions on eye movements. Our replication of their findings, in spite of the above-mentioned methodological differences, indicates that the relation between RT and instruction angle is a robust visuomotor phenomenon.

The findings for experiment one are in accord with the MRM and can also be explained via Cisek and Scott's RSH (1999). Specifically, response latencies could reflect the imagined rotation of a movement vector or a process in which distributed peaks of activation evolve over the premovement period. Importantly, however, the results for experiment two reveal a non-linear relation between RT and instruction angle, a pattern of results that is not in line with a strict interpretation of the MRM. In particular, the MRM asserts that the imagined rotation of a movement vector is an analog process wherein successive movement directions are maintained until the correct movement direction is identified. The speed of such an analog process cannot be modified. As demonstrated by Georgopoulos and Massey (1987), an analog process of mental rotation is predicted for perceptually familiar (e.g., 90°) as well as less familiar (e.g., 30°) angles. In contrast to the MRM, the RSH states that the rate of response substitution is determined by the disparity between competing neural distributions. We suggest that the rate of this process is further influenced by the perceptual familiarity of the instruction angle. More specifically and as we discuss in subsequent paragraphs, the onset of the target stimulus initiated the sequential development of two response alternatives (i.e., one in the direction of the stimulus and the other in the direction of the response), and the rate at which the VMR response was planned and executed was determined by the disparity between these alternatives as well as perceptual expertise. As such, when the stimulus-driven and the VMR response elicit a degree of dimensional overlap (i.e., 0° and 5°)

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[3] 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 et al., 1990). In terms of the present work, such commonality is determined by the spatial disparity between the stimulus-driven and the VMR response.

or when the requisite transformation involves a perceptually familiar angle (i.e., 90° and 180°), motor output is characterized by more efficient and effective response planning and movement execution relative to situations wherein the angular disparity between the stimulus-driven and VMR responses is disparate from one another (i.e., 0° and 120°) or when the transformation involves a perceptually unfamiliar angle (i.e., 70° and 105°).

We first discuss the pattern of results for VMR responses involving perceptually unfamiliar angles. Importantly, the contention that response parameters were influenced by the angular disparity between the standard and VMR responses is consistent with previous work demonstrating that motor planning areas integrate available sensory information to specify the metrics (e.g., the trajectory of the hand) of multiple potential actions while simultaneously accumulating evidence to determine which action is most appropriate (Bastian et al., 2003; Cisek and Kalaska, 2005; Erlhagen and Schöner, 2002; Ioannides et al., 2005; see also Cisek, 2006, 2007). When potential movement outcomes are disparate from one another, the distribution of neural activity reflects discrete, mutually exclusive peaks of activation. In contrast, when movement outcomes are closer together, they form a larger, continuous plateau of activation (Bastian et al., 2003; Cisek and Kalaska, 2005). The behavioral consequence of this distribution of activation is faster RTs when the spatial disparity between potential movement outcomes is reduced relative to when they are farther apart (Bock and Eversheim, 2000; Erlhagen and Schöner, 2002; Favilla, 2002; Praamstra et al., 2009). In concert with the present results, the aforementioned work demonstrates that the time required for a stimulus-driven response to decay and a movement vector to reach threshold for movement initiation (i.e., RT) is reduced when the eccentricity between potential responses is small. Although VMR tasks requiring transformations of 5°, 10°, and 15° are not of direct spatial congruence (i.e., a standard mapping task), a degree of dimensional overlap exists because the stimulus-driven and voluntary responses are in close spatial proximity to one another (Kornblum et al., 1990). As a result of this degree of similarity, the computational demands of response preparation are reduced relative to VMR responses that are more disparate from the stimulus. In this situation, extended response latencies reflect the time needed to suppress distinct, competing peaks of activation in motor planning areas. This assertion provides an explanation for the pattern of results observed for perceptually unfamiliar angles in experiments one and two, that is, response preparation and movement execution were faster and movement endpoints were less variable when the angular disparity between response alternatives was small relative to when the disparity was large. Furthermore, it is interesting to note that the mean direction of endpoints for small angles (i.e., angles less than 35°) exhibited greater disparity with the veridical instruction angle relative to larger VMR angles (i.e., angles greater than 35°; see Figs. 2 and 3). We suggest this finding is a reflection of the broad plateau of neural activation characterizing both the standard and the VMR responses. That is, when responses are in close spatial proximity to one another, motor planning areas have difficulty disentangling the merged neural activity, resulting in an overestimation of small angles.

We next turn to the results for the perceptually familiar angles of 90° and 180°. We contend that the rate and efficiency of the above-described response substitution process are further influenced by the perceptual familiarity associated with a given instruction angle. The basis for this assertion is twofold. First, the VMR task is mediated by an integrated system of perception, action, and cognition. This idea is consistent with recent behavioral work involving the anti-pointing task (Heath et al., 2009a, 2009b) as well as the affordance competition hypothesis (Cisek, 2007). Traditional theories of interactive behavior describe cognition, action, and perception as functionally and anatomically separate processes that contribute to serial processes of action selection and action specification. In contrast, the affordance competition hypothesis states that cognition, action, and perception are mediated by a unified system entailing diffuse brain regions. As such, response parameters are subject to cognitive bias, including perception-based visual cues. Second, response parameters were influenced by perceptual expertise with right angles and straight lines. Specifically, the oblique effect, a well-documented finding in the perception literature, has demonstrated that the visual system exhibits superior visual discrimination for stimuli appearing at cardinal orientations in comparison to those that appear at oblique orientations (Coppola et al., 1998; Jastrow, 1893; Howe and Purves 2005; McFarland, 1968; Nundy et al. 2000; for a review, see Appelle, 1972). In particular, McFarland (1968) reports enhanced perceptual stability for right angles and straight lines in comparison to acute and obtuse angles. The present work demonstrates that the visual system's enhanced discrimination of 90° and 180° results in more efficient and effective sensorimotor transformations. Notably, this proposal is in line with the affordance competition hypothesis' assertion that fronto-parietal networks simultaneously specify multiple potential actions for competing responses (e.g., Gibson, 1979), whereas a variety of brain areas, such as the basal ganglia and prefrontal cortex, continuously contribute information to the selection process. In terms of the present work, the results demonstrate that perceptually familiar angles led to an enhanced rate of accumulation of evidence in favor of the VMR response. As a result, perceptually familiar angles (i.e., 90° and 180°) elicited advantaged movement planning and control over the other VMR tasks studied here. It should be noted that our interpretation is also congruent with recent iterations of Goodale and Milner's (1992) influential perception action model which asserts that responses entailing top-down control are mediated via interactions between putative perception (i.e., ventral) and action (i.e., dorsal) visual pathways (for more recent review, see Milner and Goodale, 2006 or Goodale and Westwood, 2004).

The present work provides behavioral evidence that response preparation in the VMR task is not universally mediated by the imagined rotation of a movement vector. We argue that the present results provide evidence of a response substitution process, wherein participants first compute the vector between the hand and the target stimulus and then proceed to complete the requisite transformations for the appropriate motor response. We contend that the rate of response substitution is influenced by neurophysiological (i.e., the angular disparity between response alternatives) and

cognitive (i.e., the perceptual familiarity of the transformation angle) factors. Such findings suggest that visuomotor transformations are mediated by an integrated system of perception, action, and cognition.

4. Experimental procedures

4.1. Participants

Ten university students (4 males and 6 females, ages 21–37 years) volunteered to participate in experiment one and an independent sample of 10 university students (7 males and 3 females, ages 20–28 years) volunteered to participate in experiment two. All participants were self-identified as right-hand dominant, with normal or corrected-to-normal vision, and no history of neurological disorder. 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. All procedures were carried out with the understanding and written consent of the participants.

4.2. Apparatus and stimuli

Participants were seated at a virtual aiming apparatus for the duration of the experiment (for a schematic of the apparatus see Fig. 5). Visual stimuli were projected from a 30-inch flat panel monitor (DELL 3007WFP; 60 Hz, 8 ms response rate; resolution: 1280 by 960; Round Rock, TX, USA), placed upside down on the top shelf of the apparatus, to a half-silvered mirror (91.4×58.4 cm) that comprised the middle shelf. Participants pointed to virtual targets on the bottom shelf (i.e., the reaching surface) of the apparatus. The distance between both the top shelf and the mirror and the mirror 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 bottom shelf. The room lights in the experimental suite were extinguished for the duration of the testing session. Thus, the only visual cues available to participants during data collection were those projected via the computer monitor. Eye movements were monitored via a chinrest-mounted, video-based eye-tracking system set at 120 Hz (Applied Science Laboratories: H6 HS CN; Bedford, MA, USA). Participants' midline was centered on the viewing area and this position was maintained via the chinrest. All experimental events were controlled via MATLAB (7.6, The MathWorks; Natick, Massachusetts) and Psychophysics Toolbox (3.1) extensions (Brainard, 1997; Pelli, 1997).

Visual stimuli included a white fixation cross (10×10 mm) and eight white target circles (10 mm diameter), all of which were presented against a high-contrast black background. Target stimuli were located at one eccentricity (11 cm) around an imaginary concentric circle surrounding the fixation cross. 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).
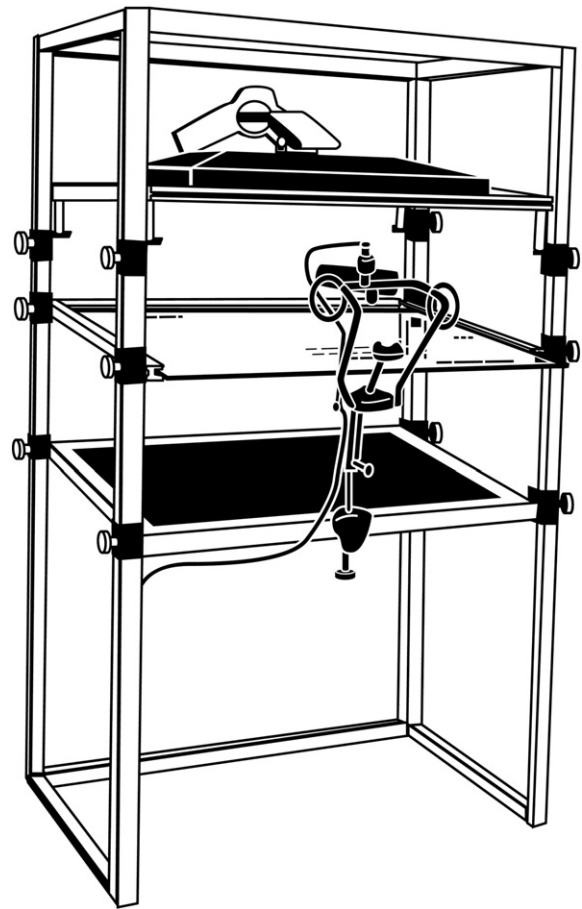

Fig. 5 – Schematic of the aiming apparatus used in this investigation.

4.3. Procedure

The procedures employed in this paradigm are comparable to those of Georgopoulos and Massey (1987). We have outlined what we believe to be some of the notable methodological differences in a separate paragraph at the end of this section.

Each testing session began with a set of general instructions. Participants were informed that they were going to complete eight blocks of 40 consecutive trials to a predetermined angle relative to a target stimulus. They were instructed that all responses should be of a clockwise departure (from the target stimulus) and were directed to refrain from making eye movements during each trial. Furthermore, they were instructed to complete their pointing response as quickly and accurately as possible. After the general instructions, participants were shown an exemplar block instruction screen that was displayed in advance of each block of trials. For example, in advance of the 30° instruction angle block, participants were shown a screen that read, "*In the next block of trials, move to a location that is rotated 30 degrees (in the clockwise direction) from the target stimulus. The line drawing below represents an angle of 30 degrees. Remember to fixate the small cross in the center of your visual field for the duration of the trial. Please report any directional errors immediately after the*

trial."[4] A pictorial representation (i.e., a line drawing) of the instruction angle was displayed in concert with the above-written instructions. 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.

In experiment one, participants performed eight blocks of trials with instruction angles of 0°, 5°, 10°, 15°, 35°, 70°, 105°, and 140°, the same set of instruction angles employed by Georgopoulos and Massey (1987). In experiment two, participants performed eight blocks of trials with equally spaced instruction angles of 0°, 30°, 60°, 90°, 120°, 150°, 180°, and 210°. Five trials were completed for each target stimulus location and instruction angle combination. Blocks were randomly ordered and the presentation of stimulus location was randomized within each block of trials. In total, participants completed eight blocks of 40 trials, for a total of 320 trials.

Each trial began with the onset of the fixation cross, and participants were instructed to fixate on this point for the duration of the trial. In addition, participants were required to align their pointing finger (i.e., right index finger) with the fixation cross (i.e., the movement start location). After a randomized fore period (1000–2000 ms), a target stimulus appeared for 50 ms in one of eight locations. Notably, the onset of the target stimulus served as the movement initiation cue. Knowledge of results (e.g., visual or verbal feedback) was not provided during the testing session. Importantly, because the oculomotor system may influence the ensuing manual response (Bock, 1986; van Donkelaar, 1997), the fixation cross was displayed for the duration of the trial and participants maintained fixation until completion of their response. Eye movements were monitored online to ensure compliance with this instruction. Trials in which a smooth or saccadic response (i.e., an eye movement) was detected were removed from the experimental sequence and the trial was re-entered into the randomized trial series.

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 eight blocks (experiment one: instruction angles of 0°, 5°, 10°, 15°, 35°, 70°, 105°, and 140°; experiment two: instruction angles of 0°, 30°, 60°, 90°, 120°, 150°, 180°, and 210°) of two trials in the practice session, for a total of 16 trials. The practice session took approximately 15 minutes to complete and was immediately followed by the testing session. The purpose of the practice session was to familiarize partici-

pants with the instruction angles as well as the timeline of events within a trial.

Several methodological differences exist between the present work and that of Georgopoulos and Massey (1987). First, participants in the current investigation were asked to accurately point to the veridical (i.e., 0° trials) or perceived (i.e., VMR trials) target location; that is, participants were required to compute both distance and direction parameters of their response. Second, participants were directed to execute their responses as quickly and accurately as possible while minimizing corrections to the trajectory. In contrast, participants in Georgopoulos and Massey's (1987) study were directed to "move in the direction they thought appropriate, but no target for the movement was provided" (p. 363). In other words, Georgopoulos and Massey (1987) did not provide instructions relating to the amplitude or speed of the response. Last, the present work prevented the influence of oculomotor information by requiring participants to fixate a central cross for the duration of each trial. Free eye movements were permitted in Georgopoulos and Massey's (1987) work.

4.4. Data collection

An infrared emitting diode (IRED) was affixed to the nail of the right index finger, and for each trial, the spatial position of the limb was sampled at 200 Hz for 2 sec via an OPTOTRAK Certus (Northern Digital Inc.; Waterloo, ON, Canada). For each trial, data capture began in time with the presentation of the target stimulus. 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. Acceleration data were similarly computed by differentiating velocity data. Movement onset was defined as the first frame in which resultant velocity exceeded 50 mm/sec for ten consecutive frames (i.e., 50 ms), and movement offset was defined as the first of ten consecutive frames in which velocity was less than 50 mm/sec. Our movement onset criterion results in an average distance of 0.52 mm (SD 0.10) between the home position and the location of the limb at movement onset. This means that our velocity threshold method defines movement onset following less than 1% of the total movement amplitude.

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[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. In line with our results for movement direction at ultimate movement endpoint, we observed a main effect of instruction angle ($Fs(7,63) = 314.73$ and 560.09, for experiments one and two, respectively), such that the direction of the trajectory increased as a function of the instruction angle. This finding reveals that participants did not adjust their reach trajectories online, rather, that reach trajectories *in toto* were specified according to the instruction angle.

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