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The Influence of Limb and Target Vision in Target-Directed and Allocentric Pointing Movements

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Abstract

The top-down nature of allocentric spatial representations (i.e., specifying target locations relative to other objects) is thought to render motor output via an offline mode of control. The present experiment tested this hypothesis by providing detailed trajectory analyses of allocentric and target-directed reaching tasks performed with and without concomitant limb vision. Allocentric tasks required reaches to a location defined by the relationship between a target and reference stimulus, whereas target-directed tasks required reaches directly to a target. Target-directed limb visible trials showed the most effective online trajectory amendments compared to their limb occluded counterparts and allocentric limb visible and occluded trials. Accordingly, I propose that target-directed reaches performed with limb vision are supported via 'fast' online visuomotor networks. In contrast, I propose that reaching in the absence of limb vision and/or to an allocentrically defined target is mediated via 'slow' offline visuoperceptual networks.

Keywords

Perception action model

Cognitive control

Online control

Allocentric

Goal-directed

Reaching

Sensorimotor

Vision

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1 Introduction

Convergent behavioural, neuropsychological, and neuroimaging evidence indicates that separate visual processing streams mediate actions and perceptions (for review see Goodale, 2014). The perception-action model (PAM) asserts that the dorsal visual pathway processes absolute visual information in an egocentric frame of reference (i.e., with respect to one's self) and supports goal-directed actions. In turn, the PAM contends that the ventral visual pathway processes relative visual information in an allocentric frame of reference (i.e., with respect to other objects) and supports top-down judgments. Further, the PAM states that the dorsal and ventral streams operate along distinct timelines. Indeed, because in a reaching/grasping task the egocentric relationship between the 'moving' limb and a stationary (or moving) target changes from moment-to-moment, the dorsal visual pathway is thought to continuously update absolute visual information in real-time (Westwood & Goodale, 2003). In contrast, allocentric relationships provide a percept that is generally invariant (i.e., temporally durable) to support recognition across multiple viewpoints (James, Humphrey, Gati, Menon, & Goodale, 2002). In demonstrating the real-time properties of movement control, neurologically intact individuals exhibit automatic trajectory amendments in response to an unexpected target 'jump' (Bridgeman, Lewis, Heit, & Nagle, 1979; Goodale, Pelisson, & Prablanc, 1986), whereas such corrections are not observed in individuals with lesions to the posterior parietal cortex (i.e., an area of the dorsal stream) (Gréa et al., 2002; Pisella et al., 2000). The absence of online corrections following a dorsal stream lesion has been interpreted as evidence of a 'slow' and cognitive mode of movement control mediated via a stable percept maintained by the ventral visual pathway (Rossetti et al., 2005).

It is important to recognize that a slow mode of cognitive control can also be observed in neurologically healthy individuals. For example, the fast and automatic target jump corrections exhibited by neurologically intact individuals (i.e., ~ 75 ms) (i.e., target-directed: see Bridgeman et al., 1979; Goodale et al., 1986) are delayed (i.e., > 160 ms) when the task requires implementing a correction mirror-symmetrical to the target jump (i.e., anti-correction; Day & Lyon, 2000; Johnson, van Beers, & Haggard, 2002). The increased latencies of anti-corrections are thought to represent the top-down (i.e., cognitive) nature of inhibiting a target-directed correction and inverting a response to a mirror-symmetrical location in reaching space. Accordingly, it has been proposed that movements requiring top-down intentional control are mediated via the slow visuoperceptual networks of the ventral stream.

In addition to target perturbation paradigms, a slow mode of control can be observed via examining the trajectories of pro- (i.e., reaching directly to a target) and antiponting (i.e., reaching mirror-symmetrical to a target) movements directed to stationary targets. For example, Maraj and Heath (2010) employed a trajectory-based regression analysis (for review see Heath, Neely, Krigolson, & Binsted, 2010b) to determine the extent to which pro- and antipointing movements employed online trajectory modifications. The regression analysis entailed computing the proportion of variance explained (i.e., R^2 values) by the spatial position of the limb at distinct stages in a trajectory (e.g., at 50% of movement time, or at the time of peak velocity/deceleration) relative to a response's ultimate movement endpoint. The basis for this technique is that weak R^2 values reflect a response that is implemented via online control mechanisms; that is, the spatial position of the limb at any stage in the trajectory does not predict a response's ultimate movement endpoint due to feedback-based amendments. In contrast, robust R^2 values indicate a response controlled primarily offline via central planning mechanisms (see also Elliott, Binsted, & Heath, 1999; Messier & Kalaska, 1999). Results showed that antipointing exhibited larger R^2 values, less accurate and more variable endpoints than their propointing counterparts and was a result the authors interpreted as evidence that the cognitive (and hence perception-based) requirements of antipointing renders a slow mode of cognitive control (Heath, Maraj, Gradkowski, & Binsted, 2009; Rossit et al., 2011; for antisaccades see Heath, Dunhma, Binsted, & Godbolt, 2010a).

The frame of reference by which a target is specified may also influence whether a reaching response is supported on- or offline. This contention is driven by work reporting that ego- and allocentrically based movements are mediated by distinct neural mechanisms. In particular, Schenk (2006) reported that patient DF – an individual with bilateral ventral stream lesions and visual agnosia (James, Culham, Humphrey, Milner, &

Goodale, 2003) – performed reaching movements commensurate to age-matched controls in an egocentrically defined task (i.e., specifying a target location relative to her hand); however, her performance in an allocentrically defined task (i.e., specifying a target location relative to a non-target stimulus) was on par to her well-documented visuoperceptual deficit. Such results were interpreted to evince that ego- and allocentrically defined tasks are mediated via dorsal and ventral visual pathways, respectively. Moreover, Thaler and Goodale (2011a) sought to determine whether ego- and allocentric representations of space influence reaching control in neurologically healthy participants. To that end, the authors had participants reach from a home position to a visual target (i.e., target-directed egocentric task), and reach to a location specified by the distance and direction between a target and a reference stimulus (i.e., allocentric task) (for schematic depiction of stimuli see **Figure 1**). In addition, target-directed and allocentric tasks were performed in conditions wherein vision of the limb (specified by a computer cursor) was available or unavailable. The limb vision manipulation provided a framework to determine whether the presence of ego-motion cues influences the frame of reference used to specify a response. The authors reported that endpoint variability was reduced when limb vision was available, and that the magnitude of this advantage was enhanced in the target-directed compared to the allocentric task. This result was interpreted as evidence that the provision of limb vision in a target-directed task provides the environment necessary to support the online control of reaches (i.e., a response mediated via the visuomotor networks of the dorsal visual pathway). In contrast, results for limb occluded trials in the target-directed task, and limb visible and limb occluded trials in the allocentric task, suggest that the absence of ego-motion cues and/or the allocentric representation of target location renders a slow mode of cognitive control.

The present investigation sought to build off Thaler and Goodale’s (2011a) work by providing detailed trajectory analyses of target-directed and allocentric tasks, and to examine whether Thaler and Goodale’s findings relate to between-task differences in sensorimotor calibration. In the first case, Thaler and Goodale’s findings and conclusions were based on the spatial distribution of movement endpoints. As a result, it is unclear whether between-task differences relate to central planning or online control mechanisms. In the second case, Thaler and Goodale employed a manipulation wherein limb vision was available from target preview to movement offset during the limb visible condition, whereas in the limb occluded condition visual feedback about the position of the effector was occluded coincident with an auditory movement imperative (Thaler & Goodale 2011a, 2011c). Thus, for the limb visible condition vision was available during movement planning and control, whereas for the limb occluded condition vision was occluded prior to movement onset as was thus unavailable during movement planning and control (i.e., see real time control hypothesis: Westwood & Goodale, 2003). This represents an important consideration in light of Prablanc and colleagues' (Prablanc, Echallier, Jeannerod, & Komilis, 1979) seminal study showing that vision of the limb and target during movement planning affords a sensorimotor calibration that optimizes the effectiveness of a response (see also Desmurget, Rossetti, Prablanc, Jeannerod, & Stelmach, 1995). As a result, it is unclear if the between-task visual condition differences demonstrated by Thaler and Goodale relate to the planning and/or control portion of the movement.

In the present investigation, participants performed target-directed and allocentric tasks (**Figure 1**) with (i.e., limb visible) and without (i.e., limb occluded) online limb vision. Importantly, for limb vision and limb occluded trials vision was available throughout movement planning and was removed only after movement onset in the latter trial-type. Further, trajectory-based regression analyses (R^2) were performed to examine between-condition differences in the extent to which responses were specified on- or offline. In terms of research predictions, if target-directed limb visible trials are mediated via fast visuomotor networks then responses should exhibit reduced endpoint variability and weaker R^2 values compared to their limb occluded counterparts; that is, such a condition should exhibit responses controlled primarily online via error-reducing trajectory amendments. Further, if the absence of limb vision and/or the specification of a response via an allocentric coordinate frame renders a slow mode of cognitive control then limb occluded trials in the target-directed task as well as limb visible and occluded trials in the allocentric task should display increased endpoint variability and larger R^2 values compared to target-directed limb visible trials. Accordingly, the present investigation provides a direct framework to determine whether the ego-motion cues and/or the frame of reference a target is specified mediates the control strategy supporting motor output.

As a secondary research objective, the present work examined whether the presence or absence of online target vision influences the manner in which target-directed and allocentric tasks are controlled. It is well known that online limb and target vision serves as the optimal environment to support online trajectory corrections (for review see Elliott et al., 2010); however, it is important to recognize that some work has shown that limb visible trials exhibit online trajectory amendments in the absence of target vision (Heath & Westwood, 2003; Heath, Westwood, & Binsted, 2004; Westwood & Goodale, 2003). Specifically, Heath (2005) had participants perform limb visible and occluded reaches in conditions wherein the target was visible (i.e., full-vision), occluded at movement onset (i.e., open-loop), or occluded at, or sometime before (e.g., 2,000 ms) response cuing (i.e., delay). The author found that limb visible trials exhibited evidence of online trajectory amendments (i.e., weak R^2 values), whereas limb occluded trials did not (i.e., robust R^2 values), and this pattern of results was independent of whether or not the target was visible during the response. It was proposed that limb vision in combination with a visual or memory-based target representation provides the requisite environment to support an online mode of control (see also Elliott & Madalena, 1987; Elliott, Jones, & Gray, 1990). To further evaluate this claim, the aforementioned target-directed and allocentric limb visible and occluded tasks were performed in full-vision and open-loop target vision conditions. The inclusion of the target vision manipulation therefore provides a platform for determining the sensorimotor conditions that influence putative control differences between target-directed and allocentric tasks.

2 Methods

2.1 Participants

Fifteen participants (8 female, age range: 19-34 years) from the University of Western Ontario community volunteered for this study. All participants were right handed with normal or corrected-to-normal vision (self-report). All participants read and signed consent forms approved by the Office of Research Ethics, University of Western Ontario, and this work was completed in accordance with the Declaration of Helsinki.

2.2 Apparatus

Participants sat at an aiming apparatus composed of three shelves (see **Figure 2**). The top shelf consisted of a computer monitor (30-inch, 16 ms response time, 60 Hz, Dell 3007WFP, Round Rock, TX, USA) that projected images onto a one-way mirror (middle shelf). The bottom shelf consisted of a solid reaching surface. The distance between each shelf was 340 mm and the optical geometry of this setup created a situation in which participants viewed stimuli displayed by the computer monitor as appearing on the reaching surface. Participants' head position was maintained via a head-cheek rest (Applied Sciences Laboratory: Model 819-2155, Bedford, MA, USA) and the one-way mirror in combination with extinguishing the lights in the experimental suite was used to prevent participants from directly viewing their reaching limb. In the place of veridical limb vision, a red light emitting diode (LED) was placed on the nail of participants' right index finger and was used to manipulate limb vision. A switch located 70 mm to the right of midline and 200 mm from the front edge of the aiming apparatus served as the start location for each trial. MATLAB (7.9.0: The MathWorks, Natick, MA, USA) and the Psychophysics Toolbox extension (ver 3.0) (Brainard, 1997) were used to control all experimental events.

2.3 Stimuli and Procedure

Visual stimuli were presented on a grey background (3 cd/m^2) and included: (1) black target circles (0 cd/m^2, 5 mm diameter), (2) a white reference circle (136 cd/m^2, 5 mm diameter) (allocentric task only), and (3) a central fixation cross (136 cd/m^2, 2.5 by 2.5

mm) (see **Figure 1**). The central fixation was located at participants' midline and 360 mm from the front edge of the aiming apparatus, whereas the reference circle was located 150 mm to the left and 50 mm in depth from the start location. Target circles were located either 30 mm to the right and 255 mm in depth (i.e., near target) or 65 mm to the right and 275 mm in depth (i.e., far target) from the home position (target-directed task) or reference circle (allocentric task)[1]. The different target circles (and eccentricities) were used to prevent participants from adopting stereotyped responses from trial-to-trial.

At the start of each trial participants were required to press the start location switch with their right index finger (i.e., the reaching limb). Once pressed, a trial sequence was initiated in which visual stimuli were presented for a randomized preview period (2000-3000 ms). A tone (2900 Hz for 50 ms) followed the preview and served as the movement imperative that instructed participants to complete reaches in each of two movement tasks. Participants were instructed to direct their gaze to the central fixation throughout a trial to equate extraretinal feedback across tasks (van Donkelaar, Lee, & Gellman, 1994). In the target-directed task participants were instructed to reach to the target circle. In contrast, in the allocentric task participants were instructed to reach a distance and direction from the home position that matched the distance and direction of the target circle relative to the reference circle (see **Figure 1**). Notably, the biomechanics of target-directed and allocentric tasks were equivalent. Target-directed and allocentric tasks were completed in two limb vision (limb visible, limb occluded) and two target vision (full vision (FV), open-loop (OL)) conditions. For limb visible trials, the LED attached to the index finger remained visible from movement planning through movement execution, whereas for limb occluded trials the LED was extinguished coincident with release of pressure from the home switch (i.e., movement onset). The purpose of the limb vision manipulation was to determine the extent to which limb vision influences the manner in which a reaching response is controlled. For the target vision manipulation, **Figure 3** shows that: (1) the target circle was visible throughout a response (i.e., FV) or (2) occluded coincident with release of pressure from the home switch (i.e., OL). Note that in the allocentric condition, the reference object followed the same timing parameters as the target object. The target vision manipulations permitted determination of the influence of target vision during movement planning and control. Participants performed each combination of task, limb vision, and target vision condition in separate blocks of trials (i.e., 8 blocks of trials). Near and far target positions were presented pseudo-randomly within each block 20 times and resulted in a total of 320 experimental trials.

2.4 Data Collection and Reduction

An infra-red emitting diode (IRED) was placed on the tip on participants' right index finger and IRED position data were tracked via an OPTOTRAK Certus (Northern Digital Inc, Waterloo, ON, Canada) at 400 Hz for 1.5 seconds following the auditory imperative. Position data were filtered offline using a second-order dual-pass Butterworth filter with a low-pass cutoff frequency of 15 Hz. A five-point central finite difference algorithm was used to calculate instantaneous velocities. Movement onset and offset were determined when resultant limb velocity exceeded and fell below 50 mm/s for ten consecutive frames, respectively.

2.5 Dependent Variables and Statistical Analyses

The magnitude of the movement vector connecting participants' start and end position (i.e., movement distance) and its angle relative to the mediolateral axis (i.e., movement direction) were computed on a trial-by-trial basis. Dependent variables included reaction time (RT: time from the imperative tone to movement onset), movement time (MT: time from movement onset to movement offset), movement distance error ($\text{Error}_{\text{dist}}$: the difference between movement distance and target distance: in mm), movement directional error ($\text{Error}_{\text{dir}}$: angular difference between movement direction and target direction: in degrees), and their corresponding variable errors (VE_{dist}: standard deviation of $\text{Error}_{\text{dist}}$, VE_{dir}: standard deviation of $\text{Error}_{\text{dir}}$)[2]. Positive and negative $\text{Error}_{\text{dist}}$ values represent an over- and undershooting bias, respectively. Positive and negative $\text{Error}_{\text{dir}}$ values represent movement vectors that were clock- or counterclockwise to the target vector, respectively. Further, for both movement distance and direction spatial correlations (i.e., R^2 values) characterizing the spatial position of the limb position at 75% of MT relative to ultimate movement endpoint were computed. These analyses were predicated on previous work indicating that movements controlled primarily online elicit weak R^2 values, whereas movements controlled primarily offline elicit robust R^2 values

(Binsted & Heath, 2004; Elliott et al., 1999; Heath, 2005; Messier & Kalaska, 1999; for review see Heath et al., 2010b). Thus, the spatial correlation analyses provided a framework to determine whether the task, limb vision and target vision conditions differentially influenced the degree to which reaches were controlled online.

Dependent variables were submitted to 2 (task: target-directed, allocentric) by 2 (limb vision: LV, LO) by 2 (target vision: FV, OL) repeated measures ANOVAs[3]. Main effects and interactions were identified as reliable at an alpha level of 0.05 or less and were decomposed via simple effects analyses. Prior to analysis, outliers were removed if RT, MT, or movement distance and direction variables were 2.5 standard deviations above or below a participant- and experimental manipulation-specific mean. This resulted in less than 5% of data being removed.

3 Results

3.1 Performance Measures

Table 1 presents means and between-participant standard deviations for all dependent variables. RT revealed a main effect of task ($F(1,14)=13.98$, $p<0.005$, $\eta_p^2=0.50$) and a task by limb vision interaction ($F(1,14)=5.84$, $p<0.05$, $\eta_p^2=0.29$). The task by limb vision interaction indicated that target-directed limb visible trials (321 ms, SD=69) produced shorter RTs than allocentric limb visible trials (356 ms, SD=72) ($t(14)=-3.59$, $p<0.005$), whereas target-directed limb occluded (332, SD=83) and allocentric limb occluded (342 ms, SD=85) trials did not reliably differ ($t(14)=-1.93$, $p=0.07$). The analysis of MT revealed main effects of task ($F(1,14)=43.99$, $p<0.001$, $\eta_p^2=0.76$), limb vision ($F(1,14)=10.07$, $p<0.01$, $\eta_p^2=0.42$), and target vision ($F(1,14)=6.63$, $p<0.05$, $\eta_p^2=0.32$). MTs were shorter for the target-directed (608 ms, SD=71) than the allocentric task (668 ms, SD=86), were shorter for limb visible (625 ms, SD=74) than limb occluded trials (650 ms, SD=83), and were shorter for OL (627 ms, SD=79) than FV (648 ms, SD=79) trials.

$Error_{dist}$ revealed a main effect of limb vision ($F(1,14)=11.82$, $p<0.005$, $\eta_p^2=0.46$) such that limb visible trials (4.0 mm, SD=13.1) overshot less than limb occluded trials (17.7 mm, SD=22.0) (**Figure 4**). Similarly, $Error_{dir}$ revealed a main effect of limb vision ($F(1,14)=23.01$, $p<0.001$, $\eta_p^2=0.62$), such that limb visible trials (0.8°, SD=1.5) had less directional error than limb occluded trials (3.3°, SD=2.0) (**Figure 4**).

Figure 5 displays the average movement trajectory and trial-to-trial endpoints for reaches to the near target separately for each task and limb vision manipulation collapsed across target vision. The figure provides a graphic representation that movement distance for target-directed limb visible reaches was less variable than their limb occluded counterparts, which in turn exhibited variability comparable to allocentric limb visible and limb occluded reaches. In terms of quantitative analysis, VE_{dist} revealed main effects of task ($F(1,14)=20.31$, $p<0.001$, $\eta_p^2=0.59$) and limb vision ($F(1,14)=13.23$, $p<0.005$, $\eta_p^2=0.49$), and interactions involving task by limb vision ($F(1,14)=8.05$, $p<0.05$, $\eta_p^2=0.37$) and limb vision by target vision ($F(1,14)=5.89$, $p<0.05$, $\eta_p^2=0.30$). The task by limb vision interaction indicated that target-directed limb visible trials (7.0 mm, SD=1.6) were less variable than their limb occluded counterparts (10.2 mm, SD=3.3) (*t*(1,14)=-3.98, $p<0.005$), whereas allocentric limb visible (11.2 mm, SD=3.3) and limb occluded (11.6 mm, SD=2.7) trials did not reliably differ (*t*(1,14)=-0.71, p=0.491) (**Figure 6**). The limb vision by target vision interaction revealed that limb visible FV trials (8.6 mm, SD=2.4) were less variable than limb visible OL trials (9.5 mm, SD=2.2) (*t*(14)=-2.18, $p<0.05$), whereas limb occluded FV (11.2 mm, SD=2.7) and OL trials (10.5 mm, SD=2.7) did not reliably differ (*t*(14)=-1.73. p=0.11). The analysis of VE_{dir} revealed main effects of task (*F*(1,14)=60.91, $p<0.001$, $\eta_p^2=0.81$) and limb vision (*F*(1,14)=18.10, $p<0.005$, $\eta_p^2=0.56$) such that the target-directed task (1.4°, SD=0.3) was less variable than the allocentric task (2.6°, SD=0.5), and limb visible trials (1.8°, SD=0.3) were less variable than limb occluded trials (2.3°, SD=0.4). Last, and given the nature of the current hypothesis, VE_{dir} did not elicit a reliable task by limb vision interaction (*F*(1,14)=0.42, p=0.529, $\eta_p^2=0.03$) (**Figure 6**).

3.2 Proportion of Endpoint Variance (R^2)

Figure 7 provides a graphic demonstration of the computation of R^2 values. For both distance and direction, the trial-to-trial spatial position of the limb at 75% of the MT was computed and correlated to the response's ultimate distance and direction endpoint. The figure demonstrates that R^2 values for the target-directed task were lower than the allocentric task for both distance and direction. In other words, the position of the limb at 75% of MT for the target-directed task provided a weaker prediction of movement endpoint than corresponding trials in the allocentric task – a result taken to evince increased online control (Heath, 2005). Further, and for both distance and direction, target-directed limb visible trials elicited lower R^2 values than their limb occluded counterparts. In the allocentric task, limb visible trials produced lower R^2 values than limb occluded trials in movement direction but not movement distance. Quantitative analysis of movement distance revealed main effects of task (*F*(1,14)=12.41, $p<0.005$, $\eta_p^2=0.47$), and limb vision (*F*(1,14)=10.11, $p<0.01$, $\eta_p^2=0.42$), and interactions involving task by limb vision (*F*(1,14)=10.26, $p<0.01$, $\eta_p^2=0.42$) and limb vision by target vision (*F*(1,14)=9.17, $p<0.01$, $\eta_p^2=0.40$). The task by limb vision interaction indicated that target-directed limb vision trials (0.50, SD=0.15) had lower R^2 values than their limb occluded counterparts (0.66, SD=0.14) ($t(14)=-4.05$, $p<0.005$), whereas allocentric limb visible (0.67, SD=0.14) and limb occluded (0.70, SD=0.08) trials did not differ ($t(14)=-1.07$, $p=0.304$) (**Figure 8**). In terms of the limb vision by target vision interaction, limb visible FV (0.54, SD=0.17) and OL trials (0.62, SD=0.15) did not reliably differ ($t(14)=-1.71$, $p=0.11$), whereas limb occluded FV trials (0.72, SD=0.08) had larger values than their OL (0.64, SD=0.11) counterparts ($t(14)=-3.21$, $p<0.01$).

Results for movement direction revealed main effects of task ($F(1,14)=29.30$, $p<0.001$, $\eta_p^2=0.68$), and limb vision ($F(1,14)=27.96$, $p<0.001$, $\eta_p^2=0.67$), and an interaction involving limb vision by target vision ($F(1,14)=6.36$, $p<0.05$, $\eta_p^2=0.31$). The target-directed task (0.61, SD=0.11) had lower R^2 values than the allocentric task (0.79, SD=0.08) (**Figure 8**). The limb vision by target vision interaction revealed that limb visible FV trials (0.58, SD=0.14) had reduced R^2 values compared to limb visible OL trials (0.69, SD=0.07) ($t(14)=-2.92$, $p<0.05$), whereas limb occluded full vision (0.76, SD=0.09) and limb occluded OL trials (0.76, SD=0.11) did not differ ($t(14)=0.11$, $p=0.91$). Last, and given the nature of the current hypothesis, we note that the regression analysis of movement direction did not elicit a task by limb vision interaction ($F(1,14)=1.87$, $p=0.193$, $\eta_p^2=0.12$) (**Figure 8**).

4 Discussion

The primary goal of the present investigation was to determine whether the frame of reference a target is specified influences the manner a response is controlled (i.e., online versus offline). To achieve that goal, participants performed target-directed and allocentric tasks in conditions wherein the limb was visible or occluded during movement execution, and detailed trajectory analyses were completed to examine the degree responses were controlled on- versus offline.

4.1 The effect of limb vision on target-directed and allocentric tasks

In accord with the extant literature (Carlton, 1981, 1992; Chua & Elliott, 1993; Heath, 2005; Heath & Westwood, 2003; Thaler & Goodale, 2011a; for review see Elliott, Helsen, & Chua, 2001) limb visible reaches were generally more accurate, less variable (i.e., more effective) and produced lower R^2 values than their limb occluded counterparts in both the distance and direction components of the movement. One explanation for the more effective endpoints and lower R^2 values of limb visible reaches is a speed-accuracy trade-off (Fitts, 1954); however, that explanation is countered by the fact that MTs for limb visible trials were shorter than limb occluded trials. A more parsimonious explanation is that limb vision afforded the opportunity to employ response-produced visual feedback to implement trajectory amendments (i.e., online control) and more accurate endpoints. In turn, results for limb occluded trials indicate that the absence of ego-motion cues rendered responses planned largely in advance of movement onset via central planning mechanisms (i.e., offline control) (Heath, 2005; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979).

For the target-directed task, the difference between limb visible and occluded trials outlined above was consistent in distance *and* direction; however, for the allocentric task the difference was limited to the direction – but not distance – component of the response. That limb vision permitted enhanced multi-dimensional feedback-based control in the target-directed – but not allocentric – task provides a general replication of Thaler and Goodale (2011a, 2011b, 2011c) and demonstrates a reduced degree of online corrections in an allocentric reaching task. Further, the differential effects of limb vision on distance and direction is congruent with evidence suggesting that each dimension is specified independently (Rosenbaum, 1980; for review see Georgeopolous, 1991).

It is, however, important to recognize that Thaler and Goodale (2011a) found that allocentric trials performed with limb vision afforded decreased endpoint variability in the distance – but not direction – component of reaches, whereas Thaler and Goodale (2011b) found reduced variability for distance *and* direction. Thus, there are discrepancies between the present results and that of Thaler and Goodale (2011a, 2011b) and within the work reported by Thaler and Goodale's group. One possible reason for the between-experiment discrepancies is that limb vision in the current investigation was provided during movement planning for limb visible and limb occluded trials. In contrast, Thaler and Goodale (2011a, 2011b) provided vision during planning and control for limb visible trials, whereas vision was occluded coincident with response cuing (2011a) or was occluded prior to response cuing (2011b) during their limb occluded trials. Thus, the advantages seen during the limb visible condition in Thaler and Goodale's work may have occurred due to an enhanced sensorimotor calibration during movement planning (see Desmurget et al., 1995; Prablanc et al., 1979) and/or an increase in feedback-based trajectory amendments during movement control; that is, the benefits of vision during planning and control cannot be disentangled from their results. In the present experiment, sensorimotor calibration was equated across limb visible and limb occluded trials and, as a result, the advantages seen during limb visible trials can be attributed to the control portion of the movement. Moreover, the conclusions made by Thaler and Goodale's group are based on endpoint variability, whereas the present experiment employed additional trajectory analyses. That variability and R^2 values follow the same pattern of results allows for a more confident statement regarding between-task differences in online control than the analysis of endpoint variability can provide alone. A second explanation for the between-experiment discrepancies is a difference in the spatial layout of the stimuli used here and that employed by Thaler and Goodale[1]. Specifically, the ratio of the distance travelled in depth to the distance travelled in the mediolateral direction was greater in the present experiment (6.37 to 1mm) than Thaler and Goodale's work (2011a) (4.15 to 1 mm), and Thaler and Goodale (2011b) varied this ratio on a trial-by-trial basis. Thus, it may be the case that the movement components were given different emphases which may have led to between-experiment differences. What is most notable in the context of the current study is that although some differences exist between my work and that of Thaler and Goodale, the convergent findings offer the same general conclusion: target-directed reaches are controlled via online trajectory amendments to a greater degree than their allocentric counterparts.

4.2 Target-directed and allocentric tasks show differences in endpoint variability and online control

As noted above, target-directed and allocentric tasks used vision of the limb to evoke online corrections, albeit to varying degrees. Although this provides evidence that online trajectory amendments are possible in each task, it does not speak to the effectiveness of such corrections. Thus, to quantify the relative effectiveness, the variability and R^2 values of target-directed relative to allocentric tasks merits consideration. In general, the target-directed task was associated with reduced endpoint variability and lower R^2 values compared to their allocentric counterparts in both distance and direction components of the movement. The increase in variability and R^2 values in the allocentric task provides evidence that, although supported via direction-based trajectory amendments (i.e., more efficient and effective limb visible than occluded trials), such amendments were less efficient and effective compared those found in the target-directed task. Further, it should be noted that target-directed limb visible trials were associated with the smallest endpoint variability and R^2 values compared to their limb occluded counterpart *and* allocentric limb visible and occluded trials. Accordingly, I propose that the presence of limb vision in the target-directed task provides the environment necessary to evoke efficient and effective online corrections. In contrast, the lack of ego-motion cues and/or the allocentric specification of a target’s location resulted in less efficient and effective online trajectory amendments. Additionally, that target-directed limb occluded trials produced comparable variability (see **Figure 5** and **6**) and R^2 values (see **Figure 8**) to allocentric limb visible and occluded trials provides evidence that the absence of ego-motion cues during a target-directed task renders a mode of control comparable to an allocentric task.

I propose that the extent to which the movement goal and target location overlap mediates the manner target-directed and allocentric responses are controlled. Specifically, I suggest that the dimensional overlap between target and goal location in the target-directed task allowed for the egocentric comparisons between limb and target necessary for fast and effective movement control mediated by the dorsal visual pathway. In turn, dissociating the target and goal location in the allocentric task required the use of top-down and perceptual based visual information and precluded the egocentric limb/target comparisons necessary for effective online trajectory amendments. This explanation is consistent with work reporting that responses directed mirror-symmetrical to a stimulus (i.e., anticorrections: Day & Lyon, 2000; antipointing: Maraj & Heath, 2010) render a slow mode of cognitive control mediated via the visuoperceptual networks of the ventral stream (Rossetti et al., 2005). Further, the goal location in the allocentric task is associated with spatial uncertainty (see Thaler & Goodale, 2011a; Thaler & Todd, 2009) – a factor that may decrease the extent a response is controlled online (Heath, Neely, & Krigolson, 2008; Izawa & Shadmehr, 2008; Loftus, Servos, Goodale, Mendarozqueta, & Mon-Williams, 2004; Schlicht & Schrater, 2007). For example, Acerbi, Vijayakumar and Wolpert (2017) had participants point to the perceived center of mass of a visual dumbbell (i.e., a bar with disks on each end) wherein the disks were equal (i.e., low uncertainty) or differently sized (i.e., high uncertainty). Specifically, in the low uncertainty trials participants were able to readily determine the movement goal as the midpoint between two disks; however, when the disks were unequally sized, the perceived center of mass was not as easily discernable and therefore uncertainty was introduced into the movement goal. The participant’s limb (represented via a cursor) was occluded for most of the movement and on a portion of trials the experimenters perturbed the cursor such that when it reappeared near the target, it was shifted and required online corrections to achieve an accurate response. Results showed that participants corrected for the visual perturbation when the goal location was certain, but only partially corrected when the goal location was uncertain. The authors concluded that the cost associated with correcting the trajectory (e.g., energy and computational load) may outweigh the potential benefit of increased accuracy and efficiency when the goal location is uncertain (see also, Knill, 2005). Importantly, the increased response latency, movement time, variability and

R^2 values of the allocentric task provide evidence that specifying the goal location was associated with high uncertainty and therefore may have rendered efficient and effective online corrections in the allocentric task too costly.

4.3 The effect of target vision on target-directed and allocentric tasks

The secondary goal of this investigation was to determine whether the presence or absence of target vision influenced the manner target-directed and allocentric tasks were controlled. This goal was based on literature suggesting that online trajectory amendments can occur in the absence of target vision (Heath, 2005; Heath & Westwood, 2003; Heath, Westwood, & Binsted, 2004; Westwood & Goodale, 2003). To that end, participants performed limb visible and occluded target-directed and allocentric tasks when the target was visible throughout the trial (i.e., full vision) or when the target was extinguished coincident with movement onset (i.e., open-loop). In terms of results, it is important to note that the presence or absence of target vision did not differentially influence endpoint variability or R^2 values for target-directed or allocentric tasks. This result is important for two reasons. First, it provides evidence that online visual target information and stored target representations are integrated and used similarly during target-directed and allocentric reaching tasks. Second, it provides evidence that the differential influence of limb vision on target-directed and allocentric tasks outlined previously was not due to and/or determined by the presence or absence of online target vision. This is particularly notable as it suggests that target-directed limb visible trials showed enhanced online control regardless of whether the target was visible – a finding indicating that the presence of ego-motion is the primary determinant of whether a response unfolds via a primarily online mode of control (see Heath, 2005).

Limb visible trials performed with online target vision produced less variable endpoints than their open-loop counterparts in the distance component of the movement; however, this decrease in variability was not accompanied by a difference in R^2 values. Such a pattern of results is in keeping with the suggestion that a stored target representation provides a durable representation to support online control; albeit with a decrease in endpoint stability (Heath, 2005). That R^2 values were unaffected by target vision is also supported by Westwood and Goodale’s (2003) hypothesis stating that the specification of a target location occurs in real time; that is, dorsal visuomotor networks specify the absolute properties of a target when a response is cued. However, in the direction component, limb visible full vision trials displayed reduced R^2 values compared to open-loop trials. Although this provides evidence that online vision of the target supports enhanced online control, it should be noted that limb visible open-loop trials proceeded with less robust R^2 values than all limb occluded trials (all *t*s(14)=-3.53 and -2.45, all ps<0.05). Further, the increase in online trajectory amendments between full vision and open-loop trials did not lead to a decrease in variability. Therefore, and in keeping with the results of the distance component, the findings evince that ego-motion cues, as opposed to target-vision, provide the environment necessary for efficient and effective online trajectory amendments to occur.

5 Conclusions

My results suggest that online vision in a target-directed task renders a reaching response specified online via the absolute and metrically precise visuomotor networks of the dorsal visual stream. Notably, this mode of control occurred regardless of whether the target was visible during the response and therefore demonstrates the importance of ego-motion cues in implementing an online mode of control. In contrast, target-directed limb occluded and allocentric limb visible and occluded trials proceeded with less efficient and effective online trajectory amendments. That target-directed limb occluded trials proceeded with comparable variability and R^2 values to allocentric trials provides evidence that in the absence of ego-motion cues, target-directed tasks behave similarly to allocentric tasks. Last, I propose that top-down control in the allocentric task resulted in motor output specified, in part, via the visuoperceptual networks of the ventral visual stream and rendered less efficient and effective online trajectory amendments. Put more directly, the present investigation demonstrates that the availability of limb vision and the reference frame in which a target is specified influences the manner a reaching response in controlled.

6 Endnotes

1. The visual stimuli used here were designed to closely match that of Thaler and Goodale (2011a) (see Figure 1 of that experiment); however, the target amplitudes differed between experiments. Specifically, the resultant target amplitudes used in Thaler and Goodale were 122 and 152 mm compared to the 257 and 283 mm amplitudes used here. The longer amplitudes are based on work demonstrating that increasing target amplitude in peripersonal space increases the reliance on feedback-based trajectory amendments (Elliott et al., 1999; Heath 2005; Heath et al., 2004; Lemay & Proteau, 2001).
2. Target vectors were computed on a trial-by-trial basis. For the target-directed condition, the magnitude (i.e., distance) and orientation (i.e., direction) of a vector connecting the participant’s start position and the target’s end position was calculated. For the allocentric condition, the magnitude and orientation of the vector connecting the reference circle to the target circle was calculated and superimposed onto the participant’s start position.
3. Since the manipulation of target amplitude was not pertinent to the hypotheses, the analysis was collapsed across this factor.

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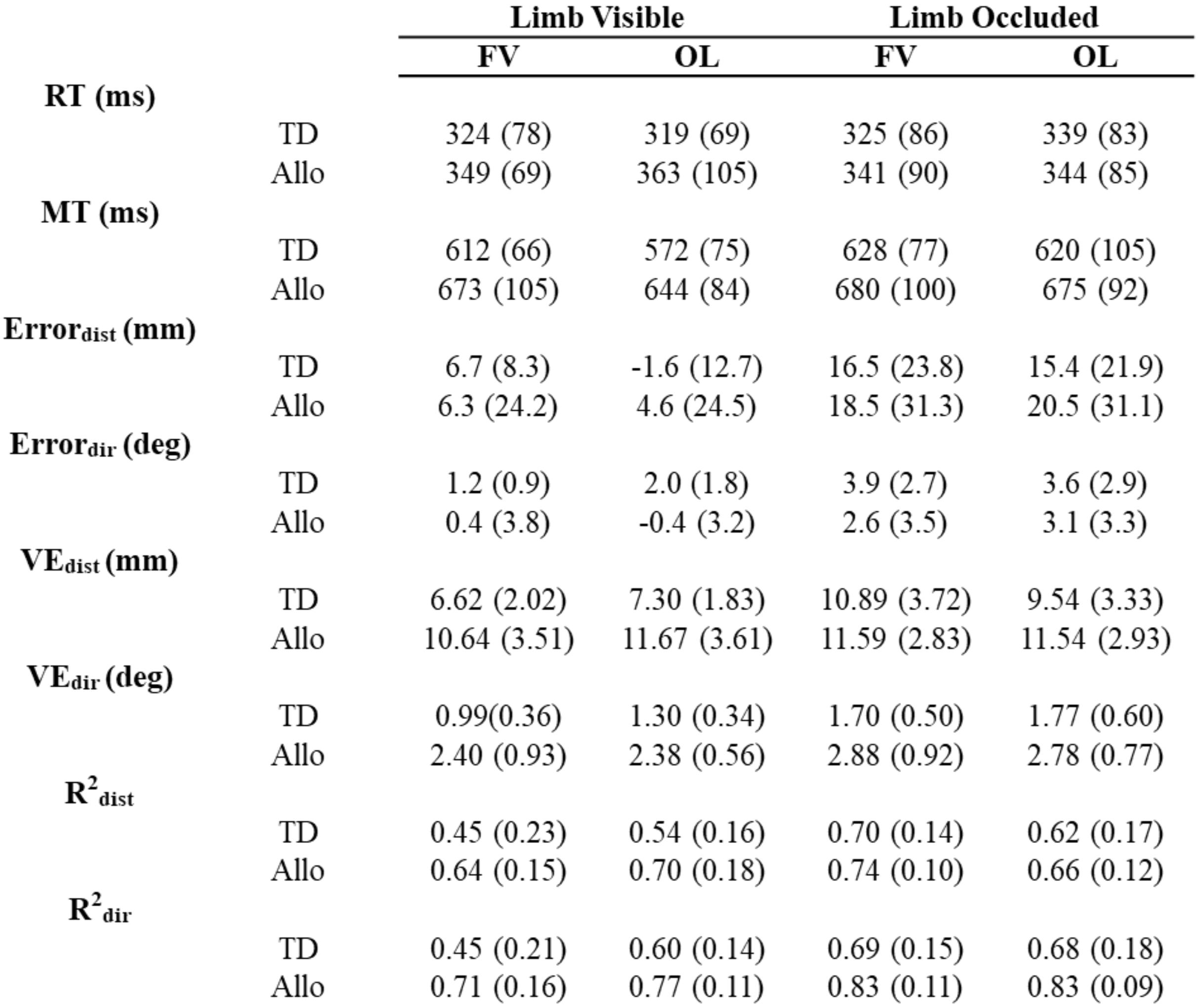
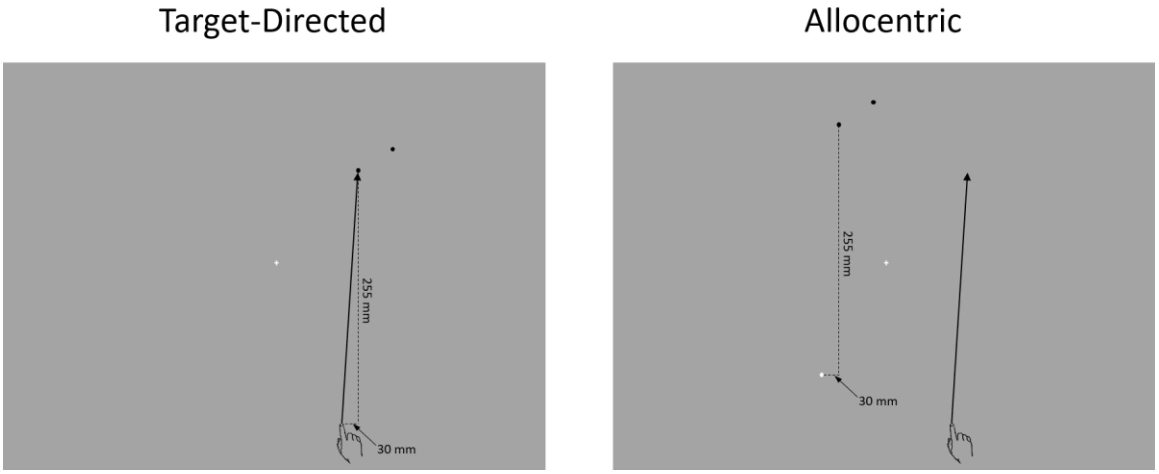
8 Tables and Figures

Table 1. Experiment means and between-participant standard deviations for target-directed (TD) and allocentric (Allo) tasks as a function of limb vision (limb visible, limb occluded) and target vision (full vision: FV; open-loop: OL) trials.



		Limb Visible		**Limb Occluded**	
		FV	**OL**	**FV**	**OL**
RT (ms)					
	TD	324 (78)	319 (69)	325 (86)	339 (83)
	Allo	349 (69)	363 (105)	341 (90)	344 (85)
MT (ms)					
	TD	612 (66)	572 (75)	628 (77)	620 (105)
	Allo	673 (105)	644 (84)	680 (100)	675 (92)
Error_{dist} (mm)					
	TD	6.7 (8.3)	-1.6 (12.7)	16.5 (23.8)	15.4 (21.9)
	Allo	6.3 (24.2)	4.6 (24.5)	18.5 (31.3)	20.5 (31.1)
Error_{dir} (deg)					
	TD	1.2 (0.9)	2.0 (1.8)	3.9 (2.7)	3.6 (2.9)
	Allo	0.4 (3.8)	-0.4 (3.2)	2.6 (3.5)	3.1 (3.3)
VE_{dist} (mm)					
	TD	6.62 (2.02)	7.30 (1.83)	10.89 (3.72)	9.54 (3.33)
	Allo	10.64 (3.51)	11.67 (3.61)	11.59 (2.83)	11.54 (2.93)
VE_{dir} (deg)					
	TD	0.99(0.36)	1.30 (0.34)	1.70 (0.50)	1.77 (0.60)
	Allo	2.40 (0.93)	2.38 (0.56)	2.88 (0.92)	2.78 (0.77)
R^2_{dist}					
	TD	0.45 (0.23)	0.54 (0.16)	0.70 (0.14)	0.62 (0.17)
	Allo	0.64 (0.15)	0.70 (0.18)	0.74 (0.10)	0.66 (0.12)
R^2_{dir}					
	TD	0.45 (0.21)	0.60 (0.14)	0.69 (0.15)	0.68 (0.18)
	Allo	0.71 (0.16)	0.77 (0.11)	0.83 (0.11)	0.83 (0.09)



Target-Directed

Allocentric

Figure 1. Stimuli used in target-directed and allocentric tasks. The black and white circles represent target and reference circles, respectively. The arrow represents a hypothetical movement vector to the near target and demonstrates that the movement endpoint, and hence biomechanics, were equivalent across the two tasks. Note that although both near and far target circles are shown, only one target circle was presented on each trial. Participants were instructed to direct their gaze to the fixation cross throughout a trial. The hand presented in this figure is for illustrative purposes only and was not visible during the experiment (see **Figure 2**). See *Stimuli and Procedures* for details.

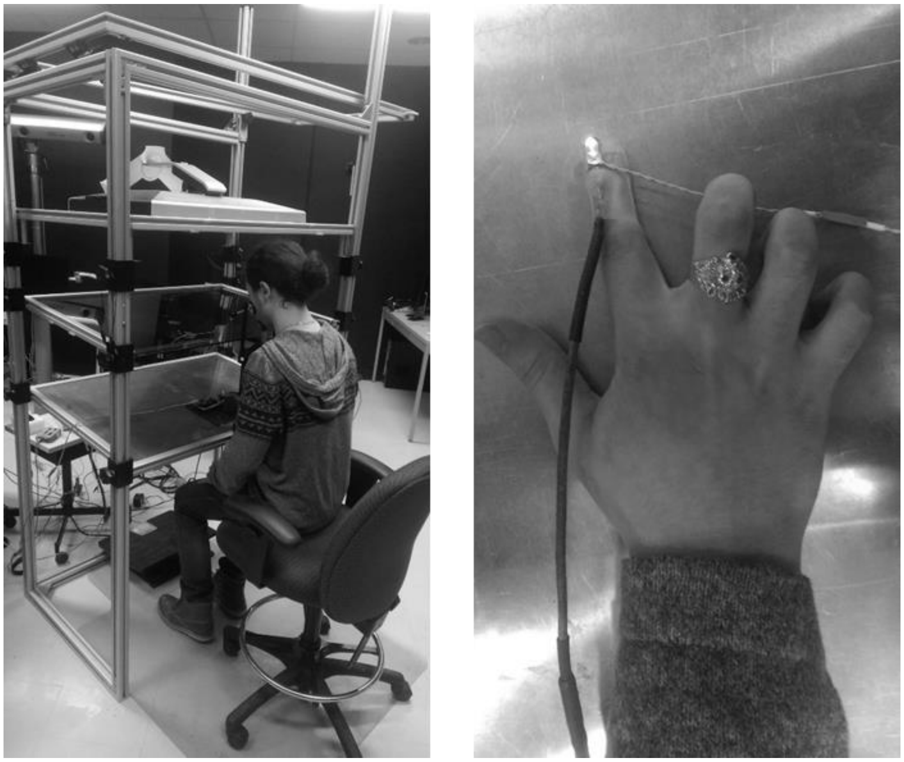


Figure 2. Aiming apparatus (left panel) and close-up view of LED and IRED placement on the reaching limb. The LED was necessary because the combination of the one-way mirror and extinction of the lights in the experimental suite prevented direct vision of the reaching limb.

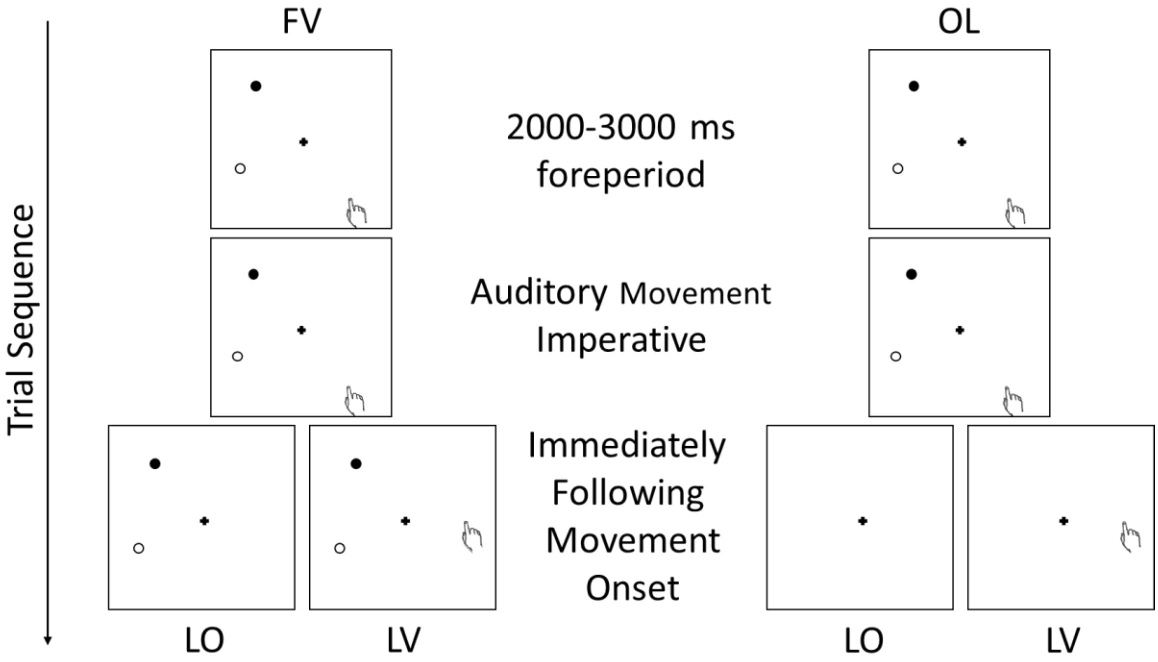


Figure 3. Schematic of limb and target vision conditions for the allocentric task (FV: target full vision; OL: target open-loop; LO: limb occluded; LV: limb visible). Note: the target-directed task included the same conditions with the exception that the target stimuli were presented rightward of the fixation cross (see Figure 1) and the stimuli used are presented in Figure 1. See *Stimuli and Procedure* for details.

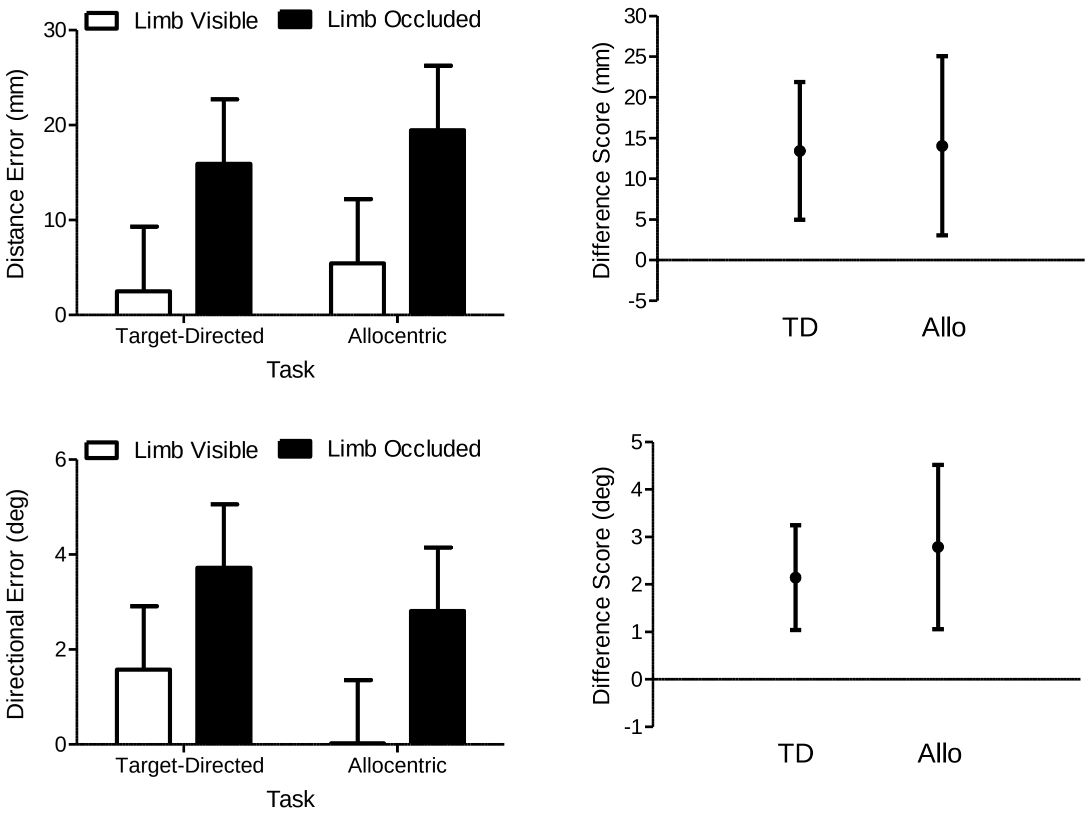


Figure 4. The left panels show systematic error in distance (top panels) and direction (bottom panels) for target-directed (TD) and allocentric (Allo) limb visible and limb occluded trials. Error bars represent 95% within-participant confidence intervals (Loftus & Masson, 1994). The right panels present the mean difference between the limb visible and limb occluded trials (i.e., limb visible minus limb occluded) in each task. Error bars represent 95% between-participant confidence intervals and the absence of an overlap between an error bar and zero represents a reliable effect that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013) (see text for details).

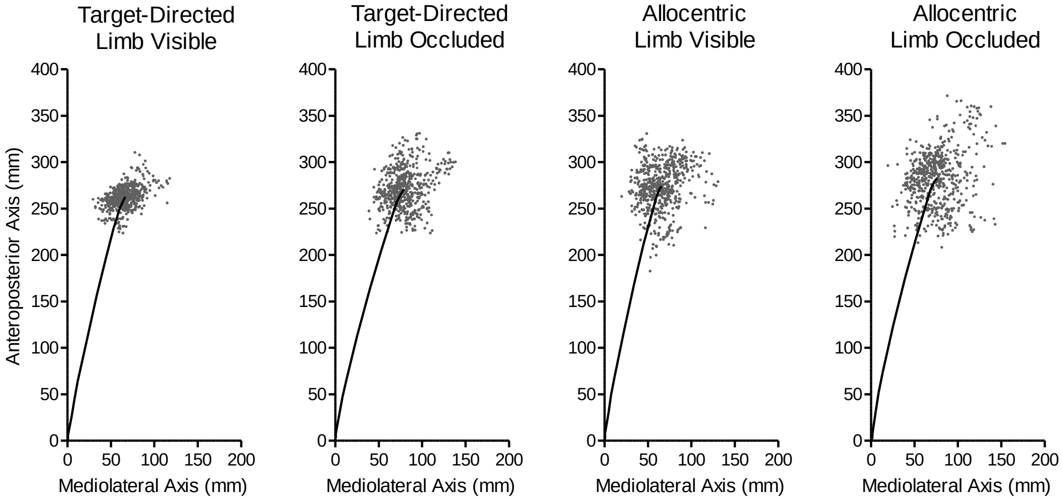


Figure 5. The solid line in each panel represents the average movement trajectory for limb visible and limb occluded trials in target-directed and allocentric tasks across all target vision conditions. In addition, each panel presents the trial-to-trial endpoints for each condition. The figure provides a graphic demonstration that endpoint variability in movement distance for target-directed limb visible trials was less than the other experimental conditions.

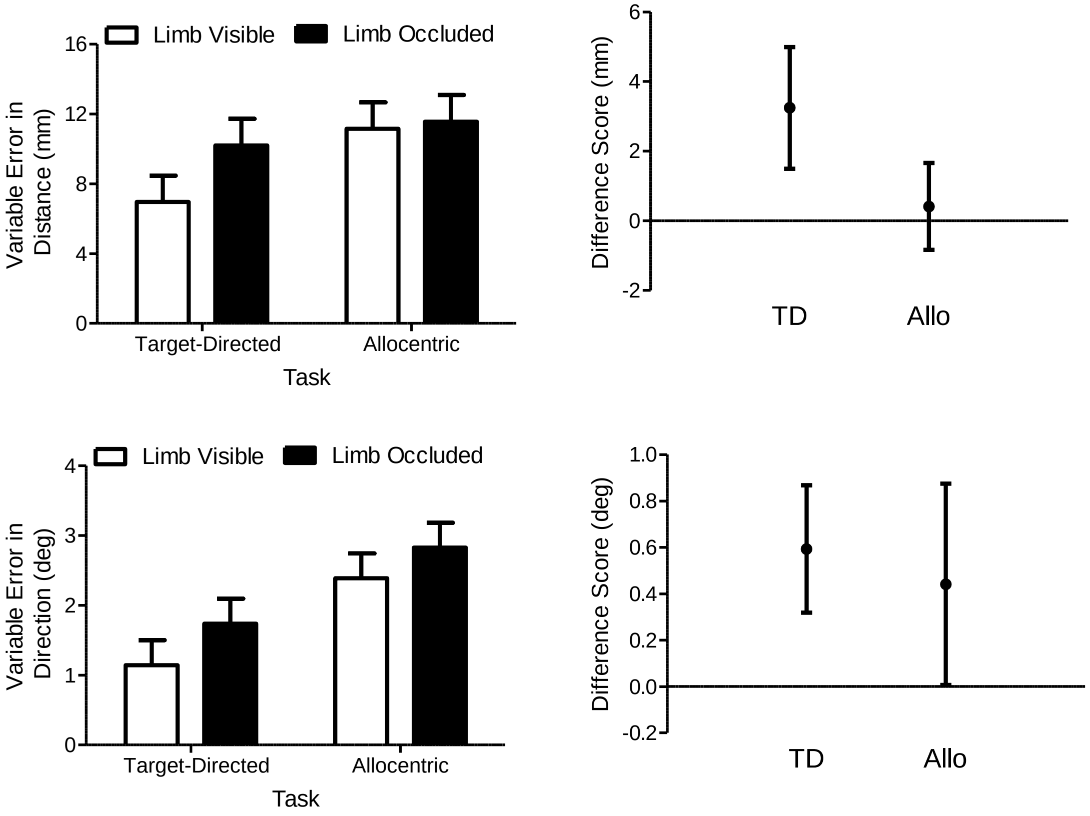


Figure 6. The left panels show variable error in distance (top panels) and direction (bottom panels) for target-directed (TD) and allocentric (Allo) limb visible and limb occluded trials. Error bars represent 95% within-participant confidence intervals (Loftus & Masson, 1994). The right panels present the mean difference between the limb visible and limb occluded trials (i.e., limb occluded minus limb visible) in each task. Error bars represent 95% between-participant confidence intervals and the absence of an overlap between an error bar and zero represents a reliable effect that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013) (see text for details).

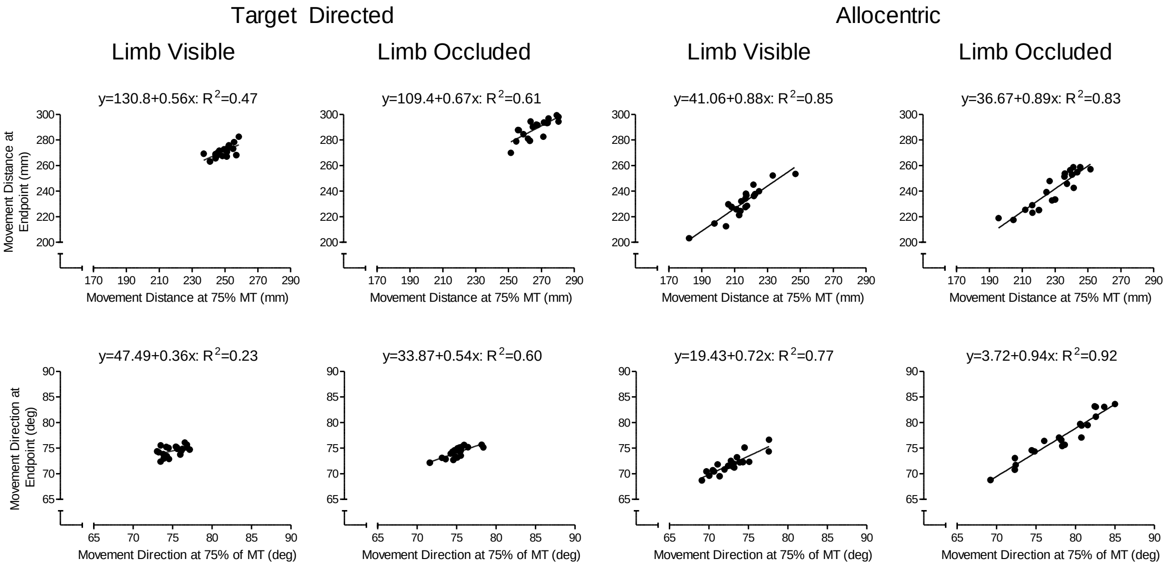


Figure 7. Exemplar participant's trial-to-trial spatial positions of the limb in distance (top panels) and direction (bottom panels) at 75% of movement time relative to each trial's ultimate movement endpoint for target-directed and allocentric tasks during full vision limb visible and limb occluded trials. The proportion of explained variance (R^2) and linear regression equations for each condition are presented at the top of each panel.

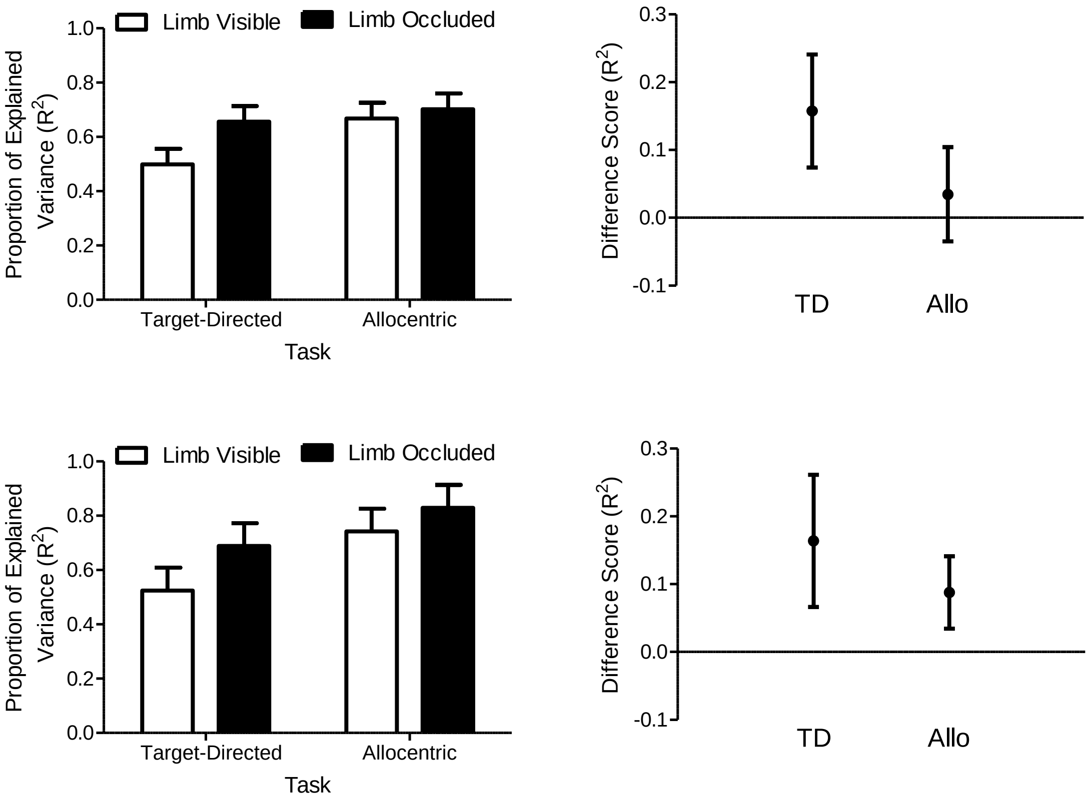


Figure 8. The left panels show proportion of endpoint variance in distance (top panels) and direction (bottom panels) explained (R^2) by the position of the limb at 75% of movement time as a function of target-directed (TD) and allocentric (Allo) limb visible and limb occluded trials. Error bars represent 95% within-participant confidence intervals (Loftus & Masson, 1994). The right panels present the mean difference between the limb visible and limb occluded trials (i.e., limb occluded minus limb visible) in each task (TD: target-directed; Allo: allocentric). Error bars represent 95% between-participant confidence intervals and the absence of an overlap with an error bar and zero represents a reliable effect that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013) (see text for details).

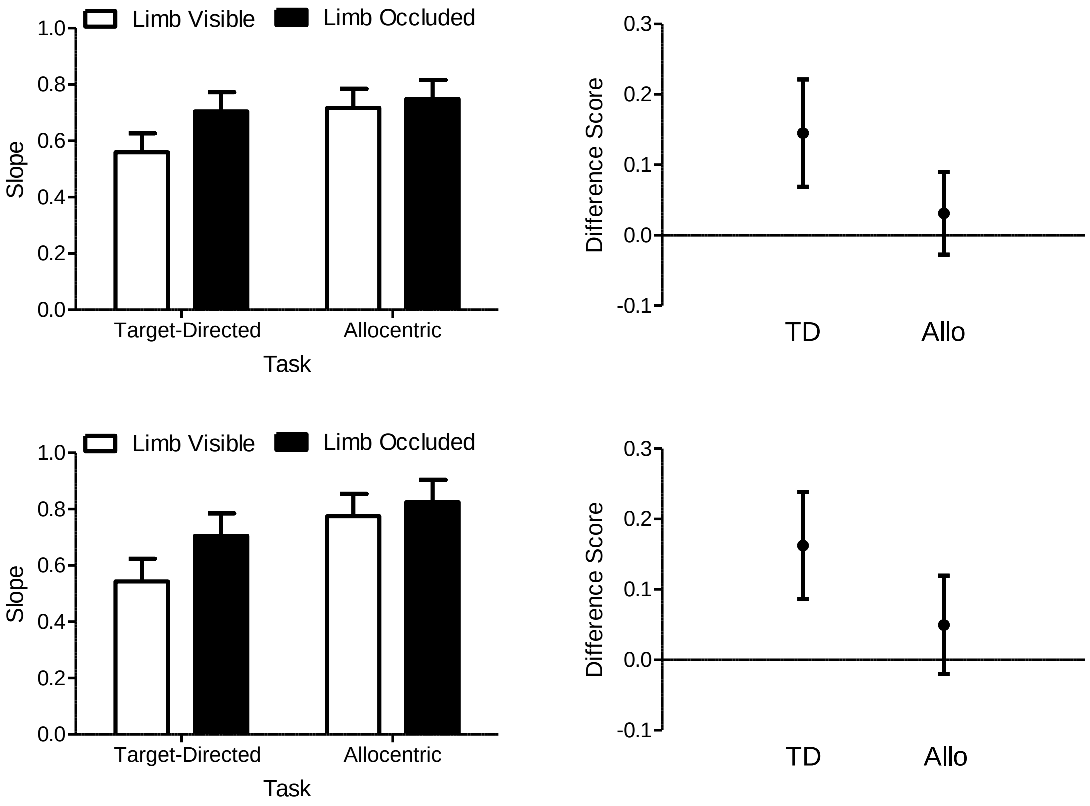


Figure 9. The left panels show the slope relating the spatial position of the limb at 75% of MT to the response's ultimate movement endpoint as a function of target-directed (TD) and allocentric (Allo) limb visible and limb occluded trials. Error bars represent 95% within-participant confidence intervals (Loftus & Masson, 1994). The right panels present the mean difference between the limb visible and limb occluded trials (i.e., limb occluded minus limb visible) in each task. Error bars represent 95% between-participant confidence intervals and the absence of an overlap with an error bar and zero represents a reliable effect that can be interpreted inclusive to a test of the null hypothesis (Cumming, 2013) (see text for details).

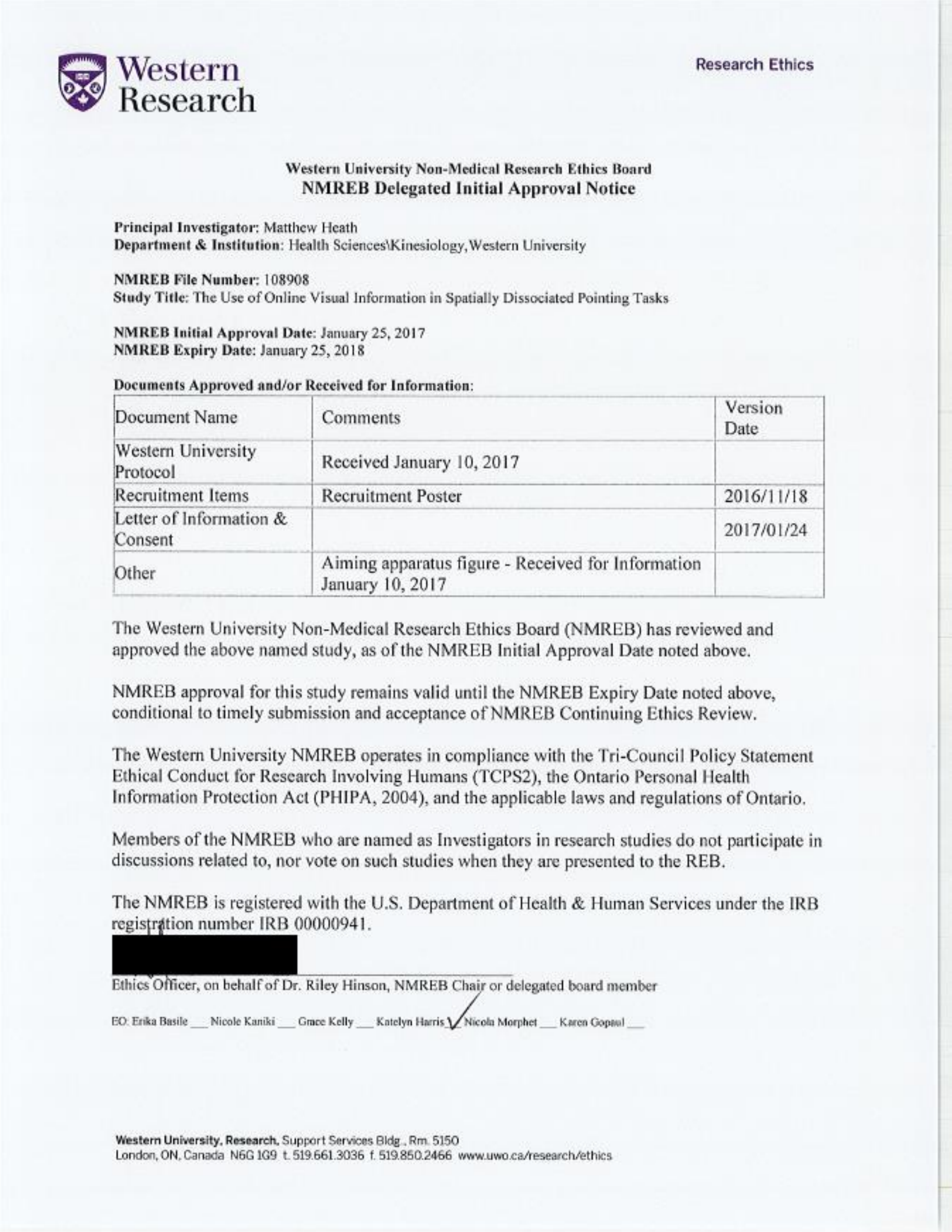
9 Appendices

9.1 Appendix A: Slope Analysis

To more fully represent the relationship between the position of the limb at 75% of MT and its position at movement endpoint, I computed the slope of the linear regression line relating the aforementioned limb position to movement endpoint (see **Figure 7**). In particular, the slope provides an approximation of how the limb's ultimate endpoint varied with limb position at 75% of MT, whereas R^2 values indicate how well this relationship represents the obtained data. Importantly, relatively high slope values provide an indication that the endpoint position is strongly influenced by the position of the limb late in the movement. However, a relatively low slope value indicates that the endpoint is not as strongly influenced by the limb position late in the movement. Results for movement distance revealed main effects of task ($F(1,14)=7.80$, $p<0.05$, $\eta_p^2=0.36$) and limb vision ($F(1,14)=15.84$, $p<0.005$, $\eta_p^2=0.53$) and task by limb vision ($F(1,14)=6.29$, $p<0.05$, $\eta_p^2=0.31$) and limb vision by target vision interactions ($F(1,14)=6.89$, $p<0.05$, $\eta_p^2=0.33$). The task by limb vision interaction revealed that for the target-directed task, limb visible trials had lower slope values (0.56, SD=0.16) than their limb occluded counterparts (0.71, SD=0.15) ($t(14)=-4.08$, $p<0.005$); however, for the allocentric task limb visible (0.72, SD=0.14) and limb occluded trials (0.75, SD=0.10) did not reliably differ ($t(14)=-1.15$, $p=0.272$) (**Figure 9**). In terms of the limb vision by target vision interaction, limb visible FV (0.54, SD=0.17) had reduced slope values than limb occluded FV trials (0.72, SD=0.08) ($t(14)=-4.72$, $p<0.001$), whereas limb visible OL trials (0.62, SD=0.15) did not differ from limb occluded OL trials (0.64, SD=0.11) ($t(14)=-0.39$, $p=0.70$).

Results for movement direction revealed main effects of task ($F(1,14)=34.04$, $p<0.001$, 0.71), limb vision ($F(1,14)=23.63$, $p<0.001$, $\eta_p^2=0.63$), and target vision ($F(1,14)=17.42$, $p<0.005$, $\eta_p^2=0.55$) and interactions involving task by limb vision ($F(1,14)=4.62$, $p<0.05$, $\eta_p^2=0.25$), limb vision by target vision ($F(1,14)=7.70$, $p<0.05$, $\eta_p^2=0.36$) and task by limb vision by target vision ($F(1,14)=6.03$, $p<0.05$, $\eta_p^2=0.30$). In decomposing the three-way interaction, it is revealed that the task by limb vision interaction occurs in FV but not OL trials. Specifically, when the target was visible throughout the trial (i.e., FV) target-directed limb visible trials (0.44, SD=0.21) had reduced slope values compared to their limb occluded counterpart (0.71, SD=0.16) (*t*(14)=-4.60, p<0.001), whereas allocentric limb visible (0.76, SD=0.13) and occluded trials (0.82, SD=0.11) did not differ from each other (*t*(14)=-1.81, p=0.09). However, when the target disappeared coincident with movement onset (i.e., OL) neither target-directed limb visible (0.65, SD=0.13) and occluded trials (0.70, SD=0.16) nor allocentric limb visible (0.79, SD=0.12) and occluded trials (0.83, SD=0.08) demonstrated differing slope values (all *t*s(14)=-1.27 and -0.77, p=0.224 and 0.454).

9.2 Appendix B: Ethics Approval



Western
Research

Research Ethics

Western University Non-Medical Research Ethics Board
NMREB Delegated Initial Approval Notice

Principal Investigator: Matthew Heath
Department & Institution: Health Sciences\Kinesiology,Western University

NMREB File Number: 108908
Study Title: The Use of Online Visual Information in Spatially Dissociated Pointing Tasks

NMREB Initial Approval Date: January 25, 2017
NMREB Expiry Date: January 25, 2018

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Western University Protocol	Received January 10, 2017	
Recruitment Items	Recruitment Poster	2016/11/18
Letter of Information & Consent		2017/01/24
Other	Aiming apparatus figure - Received for Information January 10, 2017	

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the above named study, as of the NMREB Initial Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

[redacted]

Ethics Officer, on behalf of Dr. Riley Hinson, NMREB Chair or delegated board member

EO: Erika Basile ___ Nicole Kaniki ___ Grace Kelly ___ Katelyn Harris ✓ Nicola Morphet ___ Karen Gopaul ___

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	Western Graduate Research Scholarship 2015-2017
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Related Work Experience	Teaching Assistant The University of Western Ontario 2015-2016

Publications:

Heath, M., **Manzone, J**., Khan, M., & Jazi, S. D. (2017). Vision for action and perception elicit dissociable adherence to Weber's law across a range of 'graspable' target objects. *Experimental Brain Research,* 1-10. DOI: 10.1007/s00221-017-5025-1. Published online: July 18, 2017

Heath, M., & **Manzone, J**. (2017). Manual estimations of functionally graspable target objects adhere to Weber's law. *Experimental Brain Research, 235*(6), 1701-1707.

Manzone, J., Jazi, S. D., Whitwell, R. L., & Heath, M. (2017). Biomechanical constraints do not influence pantomime-grasping adherence to Weber's law: A reply to Utz et al.(2015). *Vision Research, 130,* 31-35

Manzone, J., Cole, G. G., Skarratt, P. A., & Welsh, T. N. (2017). Response-specific effects in a joint action task: social inhibition of return effects do not emerge when observed and executed actions are different. *Psychological research, 81*(5), 1059-1071.

Welsh, T. N., **Manzone, J**., & McDougall, L. (2014). Knowledge of response location alone is not sufficient to generate social inhibition of return. *Acta psychologica, 153,* 153-159