

Role of Limb and Target Vision in the Online Control of Memory-Guided Reaches

Matthew Heath

This investigation tested the proposal that a “highly accurate” and temporally unstable stored target representation is available to the motor system for the online control of memory-guided reaches. Participants reached to a target that was: (a) visible during the response, (b) extinguished at movement onset, and (c) occluded for 0, 500, 1500 and 2,500 ms in advance of response cueing. Additionally, trials were performed with (i.e., limb visible) and without (i.e., limb occluded) vision of the reaching limb. Results showed that limb occluded trials undershot the target location in each target condition, and were characterized by a primarily offline mode of control. In contrast, limb visible trials showed a consistent level of endpoint accuracy for each target condition and elicited more online reaching corrections than limb occluded trials. It is therefore proposed that a reasonably accurate and temporally stable stored target representation can be combined with vision of the moving limb for the online control of memory-guided reaches.

Key Words: reaching, online, offline, visually guided, memory-guided

When continuous visual input is available from the reaching environment, the performer structures his/her movement to take maximal advantage of that visual information (so-called visually guided reaching). In support of this view, a myriad of studies have shown that visually guided reaches elicit a disproportional lengthening in the time spent after peak velocity (e.g., Elliott, Heath, Binsted, Ricker, Roy, & Chua, 1999b; Heath, Hodges, Chua, & Elliott, 1998; Jeannerod, 1986) and exhibit more discrete movement corrections than reaches performed without visual feedback (e.g., Chua & Elliott, 1993; Khan & Franks, 2000; Keele 1968; Meyer, Abrams, Kornblum, Wright, & Smith, 1998, Pratt & Abrams, 1996; van Donkelaar & Franks, 1991; see Elliott, Helsen, & Chua, 2001 for review). These kinematic findings are frequently held as evidence of online movement corrections computed within the posterior parietal cortex of the dorsal visual pathway (see Goodale &

Westwood, 2004, for recent review). In other words, visually guided reaches are thought to be supported by real time visuomotor mechanisms that access up-to-date visual information regarding limb and target position to implement highly accurate online limb adjustments.

Withdrawing target vision at, or for some period of time prior to movement onset, however, disrupts the normally online operation of the visuomotor system because metrically precise target information is thought to be available to dorsal visual processing mechanisms only on a moment-to-moment basis (Westwood & Goodale, 2003). Thus, it has been argued that the only source of “visual” target information available to support the online control of open-loop and memory-guided reaches is a stored sensory (specifically visual: see Elliott, Calvert, Jaeger, & Jones, 1990) target representation laid down and maintained by perceptual mechanisms residing in the inferotemporal lobe of the ventral visual pathway (Hu & Goodale, 2000; see Milner & Goodale, 1995, for extensive review). Interestingly, although a number of recent studies have shown that stored target information can support movement planning processes (Binsted & Heath, 2004, 2005; Bridgeman, Lewis, Heit, & Nagle, 2000; Heath & Rival, 2005; Heath, Rival, & Westwood, 2004a; Heath, Westwood, & Binsted, 2004b; Hu, Eagleson, & Goodale, 1999; Westwood, Heath, & Roy, 2000), a paucity of research has directly examined the use of such information for the online, feedback-based control of reaching movements. Thus, it is largely unclear whether stored target information can substitute for direct target vision to implement an effective online, feedback-based mode of reaching control.

On the one hand, withdrawing vision of the target during movement execution might yield a reaching movement planned based on visual information available prior to movement onset. In this formulation, the stored and static nature of memory-based target information does not provide the motor system a valid spatial referent for online control processes; rather, the reaching trajectory unfolds according to the spatiotemporal pattern specified by central planning mechanisms operating in advance of the response (Plamondon, 1995; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). In line with this view, a number of investigations have reported that removing visual input from the reaching environment elicits temporally symmetrical velocity profiles and very few (if any) corrections to the reaching trajectory (Carlton, 1979; Beggs & Howarth, 1970; Heath et al., 2004b; Keele, 1968). Indeed, such findings suggest that stored target information—as well as other sources of sensory input (e.g., proprioception)¹—do not provide the motor system the necessary input to operate in a primarily feedback-based mode of control.

On the other hand, some authors have argued that stored target information can be used by the motor system to support online reaching control. For instance, an influential study by Elliott and Madalena (1987) reported that “highly accurate” stored target information is available to the motor system for up to 2 s for “on-line

¹For a discussion of proprioceptive feedback in online reaching control see Redon, Hay, & Velay (1991) or Sarlegna, Blouin, Bresciani, Bourdin, Vercher, & Gauthier (2003). See also Ghez, Gordon, and Ghilardi (1995a, 1995b) for reaching control in deafferented individuals.

error reduction during the movement” (p. 36).² Similarly, Glover (2004) proposed that a “visual control representation” sustains feedback-based control when visual input from the reaching environment (target and limb) is removed (see Woodworth, 1899, for historical development of this model). Glover further proposed that the visual control representation gradually decay(s) over a period of roughly 2 s after which time reaches are “executed entirely as planned” (p. 5) (i.e., offline control). The inference here is that the motor system can use stored target information for online control if the delay between visual occlusion and movement onset is sufficiently brief (< 2,000 ms).

Elliott and Madalena’s (1987) and Glover’s (2004) supposition regarding the efficacy and temporal durability associated with the use of stored target information for online reaching control represents an intriguing idea; however, the literature offers little direct support for this proposal. That is because most of the studies probing the effect of *increasing memory delays* on reaching performance have done so in the context of having participants close their eyes during the movement (Vince, 1948), or withdrawing target vision by switching off the room lights (Elliott, 1988; Elliott & Madalena, 1987) or through the use of visual occlusion devices (e.g., blindfold or visual occlusion goggles: Darling & Miller, 1993; Elliott, Binsted, & Heath, 1999a; Heath et al. 2004b; Lemay & Proteau, 2001; Westwood, Heath, & Roy, 2001, 2003): manipulations that occlude not only vision of the target, but also vision of the limb. Indeed, withdrawing vision of the limb and the target concurrently represents an important consideration in the memory-guided reaching literature because online control might be limited to situations in which visual input from the limb is available.³ For instance, Carlton (1981) reported that withdrawing target and limb vision at the onset of a reaching response resulted in a larger accumulation in endpoint error in comparison to a situation in which only vision of the target (but not limb) was withdrawn (but see Elliott, 1988). Similarly, Berkinblit and colleagues (Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995) showed that memory-guided reaches exhibited greater 3D errors when vision of the effector was unavailable to participants than a condition wherein vision of the effector was available throughout the response (see also Adamovich, Berkinblit, Fookson, & Poizner, 1998; Adamovich, Berkinblit, Smetanin, Fookson, & Poizner, 1994). Hence, the current memory-guided reaching literature, which has emphasized the endpoint accuracy and variability of memory-guided reaches, sug-

²In a follow-up investigation, Elliott et al. (1990) reported that providing a valid precue to one of three target locations resulted in comparable response accuracy for reaching movements executed following 200, 400, 600 and 1000 ms of delay. Interestingly, endpoint error for reaching movements that were not precued accumulated in relation to the length of the delay interval.

³It has been demonstrated that direct limb vision is unnecessary to produce online corrections when a target location is perturbed during saccadic suppression (e.g., Goodale et al. 1986). This form of online control is thought to be subserved by a stimulus driven “automatic pilot” (Pisella et al. 2000). In the context of the present Introduction however, the role of limb vision for online control processes is restricted to reaches to a stationary target in peripersonal space (Previc, 1998).

gests that vision of the moving limb is paramount to obtaining an optimal level of reaching accuracy, presumably by providing an egocentric representation by which to effect error nullifying corrections to the reaching trajectory (e.g., Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Heath & Westwood, 2003; McIntyre, Stratta, & Lacquaniti, 1997, 1998; Zelaznik, Hawkins, & Kisselburgh, 1983; but see Elliott, 1988; Jeannerod, 1984; Foley, 1975).

The motivation for the present research was based on Carlton's (1981) seminal work exploring the putative importance of limb vision for online control processes and the recent work of this author and colleagues examining the impact of increasing memory delays on reaching control (e.g., Binsted & Heath, 2004, 2005; Heath et al., 2004a; Heath & Rival, 2004; Heath & Westwood, 2003; Heath et al., 2004b; Westwood et al., 2000, 2001, 2003). Specifically, Heath et al. (2004b) examined the efficacy by which stored target information might be used for online control across a range of memory delays (0, 200, 400, 600 ms of delay) in an environment that manipulated target and limb vision concurrently (via visual occlusion goggles). It was reported that open-loop and memory-guided reaches were executed based on visual information available prior to movement onset. In other words, no evidence of a time-sensitive target representation supporting online reaching control was observed: even for the briefest of memory delays (i.e., 0 ms; c.f., Heath and Westwood, 2003). In the present investigation, however, a virtual aiming task was employed so that target and limb vision could be manipulated independent of one another. As mentioned above, this treatment is warranted because of the mounting evidence suggesting that dynamic limb vision might represent the necessary input agent to use stored target information for online control (see Carlton, 1981 and McIntyre et al., 1997, 1998). Hence, in this experiment, trials in which vision of the limb was either available or unavailable during the response were factorially combined with a series of target vision conditions: (a) target visible during the response, (b) target occluded at movement onset, and (c) target occluded for 0, 500, 1,500 and 2,500 ms prior to response cueing. Importantly, the manipulation of limb vision in combination with the target delays used here provide the basis to test Elliott and Madalena's (1987) and Glover's (2004) hypothesis that stored target information provides a highly accurate and temporally limited referent for the online, feedback-based control of open-loop and memory-guided reaches.

Evaluating the Mode of Reaching Control

As indicated above, the overriding goal of this investigation was to determine whether a representation of a visual target can be stored in memory and used to support the online control of open-loop and memory-guided reaching movements. Hence, the appropriate labeling of reaching control (i.e., offline versus online) is central to this work. Recall that feedback-based control has typically been inferred from the endpoint characteristics of the reaching movement (Carlton, 1981; Elliott, 1988; Elliott & Madalena, 1987; McIntyre et al., 1997, 1998; Westwood et al., 2001, 2003), or by examining the temporal symmetry of a reaching profile (Langolf, Chaffin, & Foulke, 1976; Soechting, 1984), or by detecting discrete corrections to the reaching trajectory (Abrams & Pratt, 1993; Carlton, 1979; Elliott et al., 1999b; Heath et al., 1998; Meyer et al., 1988; Pratt & Abrams, 1996). Moreover, Kahn

and colleagues (e.g., Khan & Franks, 2001; Khan et al., 2002) have examined the variability (i.e., the within-participant standard deviations) in the spatial position of the limb at particular kinematic landmarks to determine the relative degree to which reaches are controlled via online, feedback-based control processes. Each of these techniques has its own limitations, particularly as applied to the examination of memory-guided reaching.

In the present investigation, a type of regression analysis (see Elliott et al., 1999a; Heath et al., 2004b; Krigolson & Heath, 2004; Messier & Kalaska, 1999) was used to infer the nature of limb control. This procedure examines the proportion of variability in the ultimate movement endpoint (R^2) explained by the spatial location of the limb during the early (peak acceleration: PA), middle (peak velocity: PV) and later (peak deceleration: PD) stages of the reaching trajectory. The underlying logic of this technique is that reaches executed on the basis of central planning mechanisms (i.e., offline control) should exhibit robust R^2 values at each point in the reaching trajectory as the movement unfolds without online corrections. In other words, distance and direction errors in the reaching trajectory are not corrected. In contrast, if an online, feedback-based mode of control is evoked, then there should only be a weak relationship between the spatial location of the limb at each point in the reaching trajectory and the ultimate movement endpoint. In this scenario, low R^2 values arise because distance and direction errors in the reaching trajectory are detected and corrected via feedback-based control mechanisms.

In summary, the goals of the present investigation were twofold: first, to examine the sensory input (i.e., limb visible versus limb occluded) necessary to engage stored target information for the online control of open-loop and memory-guided reaching movements; and second, to test the hypothesis that stored target information decays gradually (rather than discretely) over a 2,000 ms time frame, resulting in a monotonic reduction in the degree that reaches are controlled online. In terms of potential research outcomes, if dynamic limb vision provides the motor system the necessary input to access stored target information for online control, then certain limb vision trials (see exceptions below) should demonstrate only a weak association between the spatial location of the limb at each point in the reaching trajectory (i.e., PA, PV, PD) and the ultimate movement endpoint (i.e., an online, feedback-based mode of control). In line with Glover (2004) however, stored target information is predicted to progressively decay over a period of 2,000 ms, thereby decreasing the degree that reaches are supported by online control processes (i.e., longer target delays will result in a more robust pattern of spatial correlations).

Methods

Participants

Nine participants (5 men, 4 women) from the Indiana University community volunteered to participate in this experiment (age range: 20 to 29 years). All participants reported normal vision and were right-handed as determined by a modified version of the University of Waterloo Handedness Questionnaire (Bryden, 1977). Participants provided informed consent approved by the Office of Human Research,

Indiana University, and this study was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Apparatus

A variant of the aiming apparatus developed by Held and Gottlieb (1958) was used here. The apparatus was secured to a normal table-top and consisted of a two-sided rectangular box (70 cm high, 96 cm wide, 60 cm deep) painted flat black that was divided in half by a partially-transparent mirror angled upward 8.5° in the depth plane. A computer monitor with a 17-in diagonal display (NEC Multisync 1765: 16 ms response rate) was placed upside down on the superior surface of the apparatus so that a computer-generated image could be projected onto the mirror. When participants looked at the mirror, the optical geometry of the apparatus created an environment in which a virtual target was visible on the bottom surface of the aiming apparatus (i.e., below the mirror). A constant optical geometry was maintained via a head-chin rest (Lafayette Instruments, model 14302).

Direct viewing of the reaching limb (i.e., underneath the partially-transparent mirror) was prevented by darkening the experimental suite. In place of the veridical limb, two light-emitting diodes (white LEDs) affixed to a splint complex and attached to the pointing finger (i.e., the index finger of the right hand) were used to provide visual feedback about limb position. The LEDs (which appeared as a cross-hair) permitted instantaneous control of limb vision without altering light levels across the different experimental conditions (see below). Eprime (version 1.0) software was used to present visual stimuli and to control visual and auditory events.

Procedure

Participants were asked to complete discrete reaching movements to one of two targets as “quickly and accurately as possible” in response to an auditory initiation cue. Prior to data collection, 20 practice trials were provided to familiarize participants with the virtual aiming environment. The start of an experimental trial began once participant’s index finger depressed the home position (a microswitch) located 16 cm to the left of participant’s midline and 31 cm from the front edge of the table top. After the home position was depressed, one of two red targets (1 cm in diameter) located 28 cm (near) and 32 cm (far) to the right of the home position (and 31 cm from the front edge of the table) was projected against a high contrast black background for a 2 s preview phase. Reaching to “touch” the virtual target entailed left to right displacement of the limb in the frontal plane. Trials were completed in two limb conditions (limb visible, limb occluded) and six target vision conditions (see below). For limb visible and limb occluded trials, the LEDs affixed to the splint complex were illuminated once the home position was depressed. In both conditions, the LEDs were visible at movement planning so that the premovement calibration of limb position was equivalent (see Desmurget, Rossetti, Jordan, Meckler, & Prablanc, 1997; Prablanc, Echallier, Jeannerod, & Komilis, 1979; Rossetti, Stelmach, Desmurget, Prablanc, & Jeannerod, 1994; Vindras, Desmurget, Prablanc, & Viviani, 1998). During limb visible trials, the

LEDs remained illuminated throughout the response, thereby providing participants with continuous vision of their moving limb. In contrast, during limb occluded trials, the LEDs were extinguished with release of pressure from the home position microswitch, thus precluding online visual monitoring of the limb.

The six target vision conditions used in this investigation included: target vision (T-V), target open-loop (T-OL), and target delay conditions of 0, 500, 1,500 and 2,500 ms (TD-0, TD-500, TD-1500, TD-2500). For the T-V trials, following the 2 s target preview phase, an auditory cue signaled participants to begin their reaching movement and the target remained visible throughout the movement (i.e., for 2 s following the auditory cue). For the T-OL trials, immediately following the preview phase, the auditory cue signaled participants to begin their reaching movement and the target was extinguished once the participant's finger released the microswitch; thus target vision was occluded at movement onset. For the TD-0 trials, following the preview phase the target was extinguished coincident with the auditory movement cue; thus, vision of the aiming environment was occluded prior to movement onset and during the response. For the TD-500, TD-1500, TD-2500 conditions, the target was extinguished immediately following the preview phase, and the auditory initiation cue was provided 500, 1,500 or 2,500 ms later. Knowledge of results was not explicitly provided in any of the visual conditions; however, terminal accuracy could be evaluated when a limb visible trial was executed in a T-V condition.

The two limb vision conditions (limb visible, limb occluded) were factorially combined with the six target vision conditions to produce 12 blocks of trials. Each trial block contained 60 trials yielding a total of 720 experimental trials. Trial blocks were randomly ordered with target distance (near, far) appearing pseudo-randomly an equal number of times within each block. In advance of a change in trial blocks, a text screen was displayed to provide participants with explicit information as to the availability of limb and target vision.

Data Collection and Reduction

As mentioned above, a splint complex was attached to the pointing finger. In addition to containing dual LEDs, the splint contained a single infra-red emitting diode (IRED). Three-dimensional kinematic data of IRED position were sampled at 200 Hz for 2 sec following the auditory initiation cue using an Optotrak 3020 (NDI, Waterloo, ON). Off-line, displacement data were filtered via a second-order dual-pass Butterworth filter employing a low-pass cut-off 15 Hz. Instantaneous velocities were calculated by differentiating the displacement data using a three-point central finite difference algorithm and velocity data were differentiated to obtain acceleration information. Displacement, velocity, and acceleration profiles were used to identify performance and kinematic measures (see below). Trials missing data for technical reasons (i.e., IRED out of sight) were excluded from further data analysis, and accounted for no more than 1% of trials for any participant.

The frame associated with movement onset was marked by an analog signal driven by the home position microswitch (i.e., release of pressure from the micro-switch). Movement offset was the frame at which the instantaneous velocity fell

below 50 mm/s and stayed below this level for ten consecutive frames (50 ms). Dependent variables included: reaction time (RT: time from auditory initiation tone to movement onset), movement time (MT: time between movement onset and offset), peak velocity (PV: maximum resultant velocity between movement onset and offset), time to peak velocity (TPV: time between movement onset and maximum resultant velocity), time after peak velocity (TAPV: time between maximum resultant velocity and movement offset), constant error in the primary (CE_p : mediolateral) and secondary (CE_s : anteroposterior) movement directions and their associated variable error values (VE_p , VE_s). Note that a negative CE_p indicates an undershooting error, whereas a positive CE_p indicates an overshooting error. In terms of CE_s , a negative value indicates that the endpoint was biased proximally in the depth plane (i.e., reaching below the target), whereas a positive CE_s indicates an endpoint bias in the distal depth plane (i.e., reaching above the target).

A regression technique (see Heath et al., 2004b) was employed to examine the putative contributions of offline and online control processes across the different limb and target vision conditions. In brief, this technique examines the proportion of variability (R^2) in endpoint position explained by the position of the limb at peak acceleration (PA: maximum resultant acceleration between movement onset and offset), peak velocity (PV: see above), and peak deceleration (PD: maximum resultant deceleration between movement onset and offset). If participants employ an online, feedback-based control strategy, then the position of the limb at any point in the reaching trajectory need not strongly predict the ultimate movement endpoint as programming errors in distance and direction are amended online (e.g., the undershooting or overshooting or the proximal or distal bias in the reaching trajectory is detected and corrected). If, however, participants plan their reaching movement primarily offline, then distance and direction errors associated with the middle and later stages of the movement should be significantly related to the ultimate movement endpoint. R^2 values for primary and secondary movement directions were computed at PA, PV, and PD for each participant using the 30 reaches made in each of the experimental conditions (two limb conditions, six target vision conditions, two target distances).

Results

An alpha-level of 0.05 was used to interpret all omnibus tests. Where appropriate, F -statistics were corrected for violations of the sphericity assumption using the appropriate Huynh-Feldt correction (corrected degrees of freedom are reported to one decimal place). Simple effects analyses and a Bonferroni correction for multiple comparisons ($\alpha = 0.05$) were used to decompose significant effects/interactions. Only significant effects are reported. In most cases, means and between-subjects standard error of the mean are presented below.

Performance Measures

RT, MT, CE, and VE data were submitted to 2 (Limb Vision: limb visible, limb occluded) by 6 (Target Vision: T-V, T-OL, TD-0, TD-500, TD-1500, TD-2500) by 2 (Target Distance: near, far) repeated-measures analyses of variance. The analysis

of RT did not yield significant effects or interactions (Mean RT = 200 ± 15 ms). The MT analysis elicited main effects for Limb Vision, $F(1,8) = 8.19, p < .03$, and Target Distance, $F(1,8) = 40.43, p < .001$. Limb visible trials (426 ± 30 ms) were slower than limb occluded trials (396 ms ± 26 ms), and as expected, MT increased in relation to target distance (near target = 404 ± 27 ms, far target = 418 ± 29 ms) (see Table 1 for further details).

The analyses of CE in the primary and secondary movement directions exhibited a significant effect of Limb Vision [$CE_p: F(1,8) = 13.76, p < .01$; $CE_s: F(1,8) = 10.92, p < .02$], a Limb Vision by Target Vision interaction [$CE_p: F(5,40) = 4.22, p < .01$; $CE_s: F(5,40) = 2.98, p < .05$], and a Limb Vision by Target Distance

Table 1 Mean Movement Time, Peak Velocity, Time to Peak Velocity, and Time After Peak Velocity as a Function of Limb Vision and Target Vision

Kinematic measure	Target vision						Row mean
	T-V	T-OL	TD-0	TD-500	TD-1500	TD-2500	
MT							
Limb visible	434 (33)	395 (32)	439 (34)	413 (32)	444 (30)	431 (30)	426
Limb occluded	402 (28)	376 (20)	396 (31)	401 (28)	395 (30)	405 (29)	396
PV							
Limb visible	1581 (121)	1692 (113)	1519 (131)	1601 (135)	1505 (109)	1568 (130)	1578
Limb occluded	1565 (93)	1588 (95)	1542 (107)	1542 (126)	1558 (141)	1506 (111)	1550
TPV							
Limb visible	209 (15)	206 (14)	222 (16)	218 (16)	222 (16)	222 (15)	216
Limb occluded	210 (9)	193 (9)	206 (15)	208 (13)	206 (14)	211 (12)	206
TAPV							
Limb visible	225 (21)	189 (21)	217 (19)	195 (20)	222 (24)	209 (26)	210
Limb occluded	191 (23)	183 (15)	190 (18)	193 (17)	188 (21)	194 (21)	190

Note. MT, mean movement time in ms; PV, peak velocity in mm/s; TPV, time to peak velocity in ms; TAPV, time after peak velocity in ms. Values in parentheses represent between-subjects SEM.

interaction [CE_p : $F(1,8) = 8.05, p < .03$; CE_s : $F(1,8) = 17.49, p < .001$]. As shown in Figure 1, limb visible trials ($CE_p = 2 \pm 2$ mm: $CE_s = 2 \pm 4$ mm) were more accurate than limb occluded trials ($CE_p = -23 \pm 7$ mm: $CE_s = 12 \pm 5$ mm). Decomposition of the Limb Vision by Target Vision interaction indicated that limb occluded trials

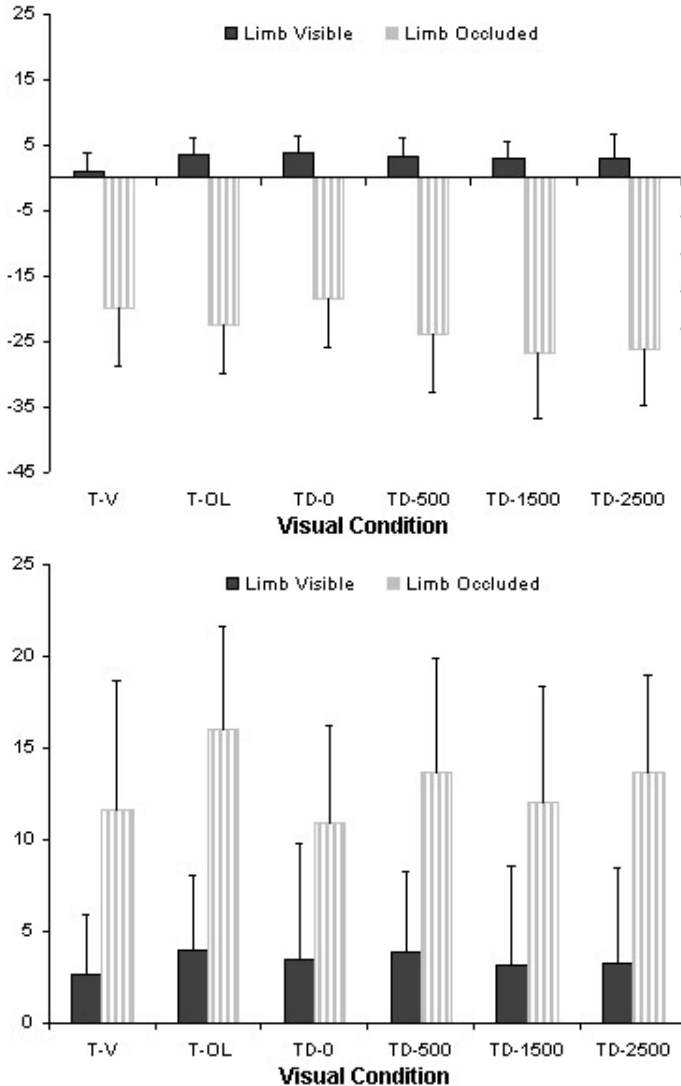


Figure 1—Mean constant error (mm) in the primary (top) and secondary (bottom) movement directions as a function of limb vision and target vision. For comparative purposes, note that the ordinates are not equivalent—error in the primary movement direction was greater than the secondary movement direction. Error bars represent SEM.

were not influenced by the different target vision conditions [CE_p : $F(5,40) = 1.69$, $p > .05$; CE_s : $F(5,40) = 1.45$, $p > .05$]. In contrast, limb visible trials were most accurate in the T-V condition relative to the other target vision conditions, which did not differ from one another [CE_p : $F(5,40) = 4.24$, $p < .01$; CE_s : $F(5,40) = 2.88$, $p < .05$]. In terms of the Limb Vision by Target Distance interaction, target distance did not influence the accuracy of limb visible trials [CE_p : $t(8) = .49$, $p > .05$; CE_s : $t(8) = .71$, $p > .05$]; however, limb occluded trials to the near target were more accurate than limb occluded trials to the far target [CE_p : $t(8) = 2.90$, $p < .01$; CE_s : $t(8) = 3.32$, $p < .01$].

The analyses of VE in the primary and secondary movement directions yielded a main effect for Limb Vision [VE_p : $F(1,8) = 77.81$, $p < .001$; VE_s : $F(1,8) = 30.69$, $p < .001$]. In addition, VE in the primary movement direction elicited a significant effect of Target Distance, $F(1,8) = 10.34$, $p < .03$. Figure 2 shows that limb visible trials ($VE_p = 9 \pm 0.7$ mm, $VE_s = 6 \text{ mm} \pm 0.7$ mm) were less variable than limb occluded trials ($VE_p = 15 \pm 1.1$ mm, $VE_s = 9 \pm 0.4$ mm). In keeping with the well-reported “distance effects” (e.g., Elliott & Lee, 1995; Lemay & Proteau, 2001) endpoint variability increased with target distance in the primary movement direction (near target = 8 ± 0.9 mm, far target = 14 ± 1.0 mm).

Kinematic Measures

PV, TPV, and TAPV were analyzed via 2 (Limb Vision: limb visible, limb occluded) by 6 (Target Vision: T-V, T-OL, TD-0, TD-500, TD-1500, TD-2500) by 2 (Target Distance: near, far) repeated-measures analyses of variance. The results for PV and TPV elicited significant effects for Target Distance [PV: $F(1,8) = 71.50$, $p < .001$; TPV: $(1,8) = 22.20$, $p < .01$], such that the magnitude and timing of trials to the near target (1478 ± 100 mm/s; 205 ± 12 ms) was less than the far target (1650 ± 116 mm; 217 ± 13 ms). In terms of TAPV, a significant effect of Limb Vision was observed, $F(1,8) = 9.30$, $p < .02$: TAPV for limb visible trials (210 ± 19 ms) was greater than for limb occluded trials (190 ± 13 ms).

Proportion of Endpoint Variance (R^2) Explained at PA, PV and PD

Recall that these analyses (primary and secondary movement directions) examined the proportion of variance in movement endpoints explained by the position of the limb at PA, PV, and PD. The R^2 values used in these analyses were subjected to 3 (Kinematic Marker: PA, PV, PD) by 2 (Limb Vision: limb visible, limb occluded) by 6 (Target Vision: T-V, T-OL, TD-0, TD-500, TD-1500, TD-2500) by 2 (Target Distance: near, far) repeated measures ANOVA.

Figure 3 depicts the R^2 values (primary movement direction) for an exemplar participant (P1) when reaching to the far target in each of the limb vision and target vision conditions. What is demonstrated in this figure is that R^2 values for limb visible trials (left panels) across target vision conditions are relatively small at each kinematic marker. In contrast, limb occluded trials (right panels) across the target vision conditions demonstrate robust R^2 values at the later occurring time points (i.e., PV and PD). In other words, the spatial location of the limb at PV and PD during limb occluded—but not limb visible—trials was well-related to the ultimate movement endpoint.

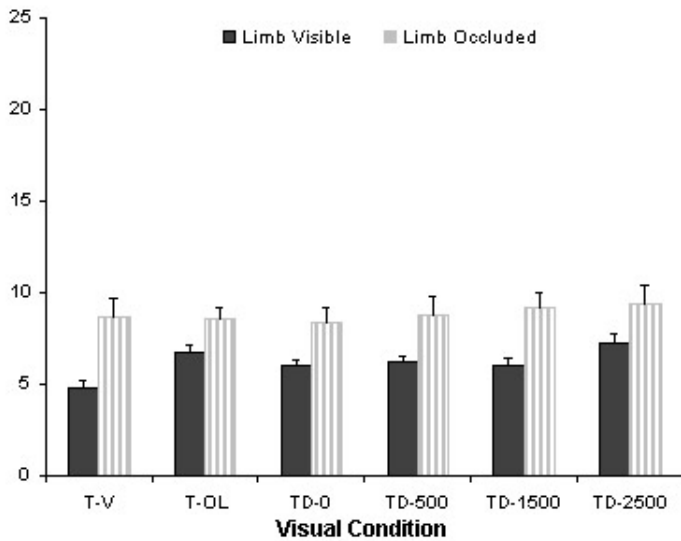
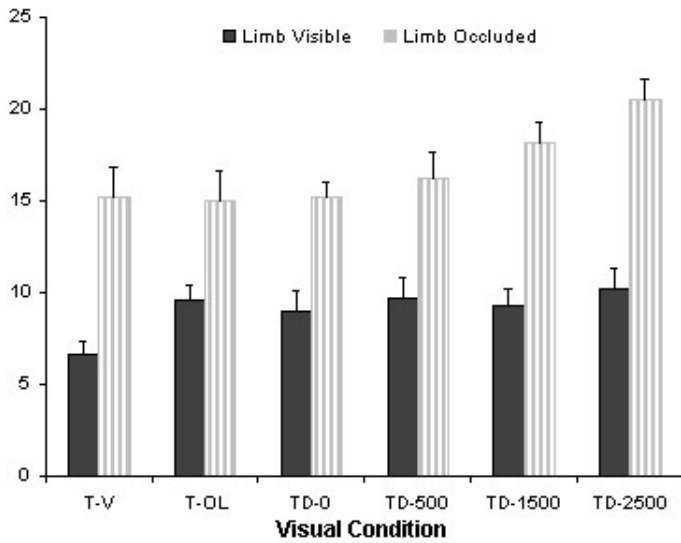
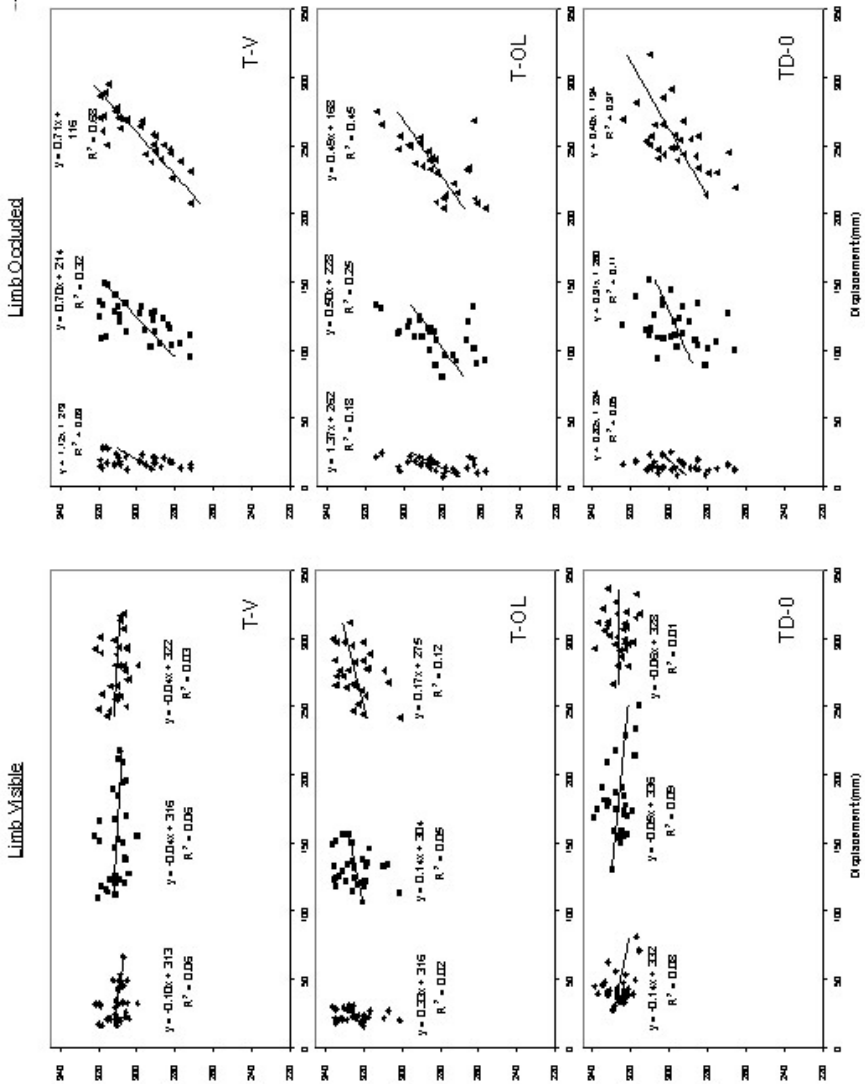


Figure 2—Mean variable error (mm) in the primary (top) and secondary (bottom) movement directions as a function of limb vision and target vision. Error bars represent SEM.



(continued)

Figure 3—The proportion of variance (R^2) in movement endpoints in the primary movement direction explained by the position of the limb at three kinematic markers (PA = peak acceleration, PV = peak velocity, PD = peak deceleration) is presented for an exemplar participant (P1) as a function of limb vision (limb visible = left panels, limb occluded = right panels) and target vision. Trials depict reaches to the far target.

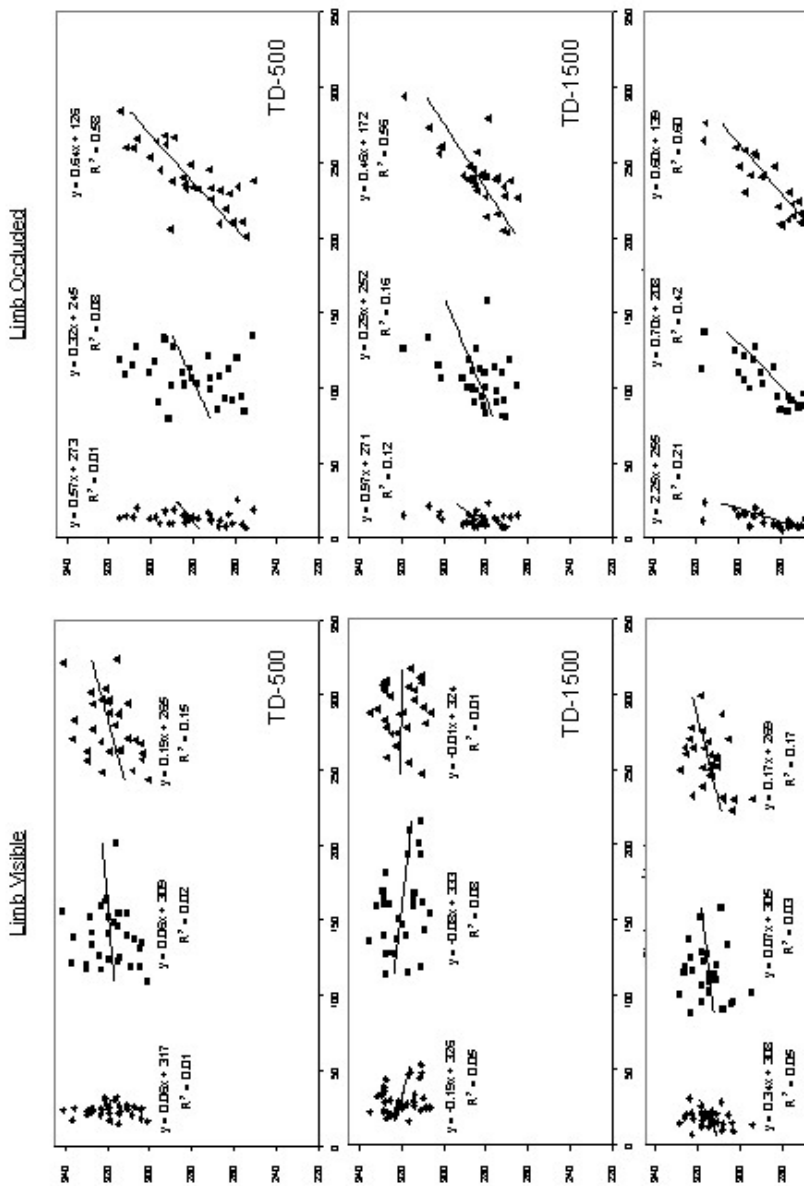


Figure 3—(continued)

The group analysis of R^2 values in the primary movement direction mirror the description above, eliciting significant effects of Kinematic Marker, $F(1.1,8.9) = 215.00, p < .001$, Limb Vision, $F(1,8) = 40.96, p < .001$, Target Distance, $F(1,8) = 6.14, p < .04$, and interactions involving Kinematic Marker by Limb Vision, $F(1.0,8.9) = 35.42, p < .001$, and Kinematic Marker by Target Distance, $F(1.2,9.9) = 9.60, p < .01$. The examination of the effect of Kinematic Marker revealed that R^2 values increased from PA to PV [$t(8) = 8.40, p < .001$], and from PV to PD [$t(8) = 15.35, p < .001$] ($PA = 0.08 \pm .01, PV = 0.14 \pm .02, PD = 0.39 \pm .03$). In terms of the Kinematic Marker by Limb Vision interaction, limb visible and limb occluded trials did not differ at PA [$t(8) = 1.21, p > 1.0$], beyond this, limb visible trials exhibited smaller R^2 values relative to limb occluded trials [PV: $t(8) = 4.37, p < .01$; PD: $t(8) = 7.03, p < .001$] (Figure 4). The Kinematic Marker by Target Distance interaction indicated that near and far targets did not differ at PA [$t(8) = 0.53, p > .60$] or PV [$t(8) = 1.45, p > .18$]; however, at PD, R^2 values for the near target were greater than the far target [$t(8) = 3.21, p < .01$].

R^2 values in the secondary movement direction yielded significant effects of Kinematic Marker, $F(2,16) = 566.70, p < .001$, Limb Vision, $F(1,8) = 23.83, p < .01$, and an interaction involving Kinematic Marker by Limb Vision, $F(2,16) = 8.30, p < .01$. In general, it was found that R^2 values increased from PA to PV [$t(8) = 8.91, p < .001$] and from PV to PD [$t(8) = 27.15, p < .001$] ($PA = 0.08 \pm .01, PV = 0.28 \pm .03, PD = 0.75 \pm .02$). The Kinematic Marker by Limb Vision interaction demonstrated that limb visible and limb occluded trials exhibited similar R^2 values at PA [$t(8) = .31, p > .75$]; however, limb occluded trials exhibited more robust R^2 values at PV [$t(8) = 3.93, p < .01$] and PD [$t(8) = 7.94, p < .001$] (Figure 4).

Discussion

Limb Visible Versus Limb Occluded Trials

Limb visible trials marginally overshot the target location in the primary movement direction and exhibited minor error in the secondary movement direction (i.e., reaching slightly above the target). In contrast, limb occluded trials significantly undershot the target location in the primary movement direction and showed considerable error in the secondary movement direction (i.e., reaching significantly above the target). In addition, endpoint variability associated with limb visible trials was less than limb occluded trials. The finding that limb visible trials were more accurate than limb occluded trials is in keeping with Carlton (1981) and more recent work examining the importance of limb vision for endpoint accuracy and consistency (e.g., Berkinblit et al., 1995; Chrurchill et al., 2000; Heath & Westwood, 2003; McIntyre et al., 1997). It is, however, important to note that at least three studies have reported that online vision of the hand is of minor importance in attaining a high level of endpoint accuracy for open-loop or memory-guided reaches to a stationary target in peripersonal space (Elliott, 1988; Foley, 1975; Jeannerod, 1986). According to Proteau and Cournoyer (1990), however, the absence of a beneficial limb vision effect might be restricted to situations wherein insufficient practice precludes effectively integrating visual feedback of the limb in an impoverished reaching environment.

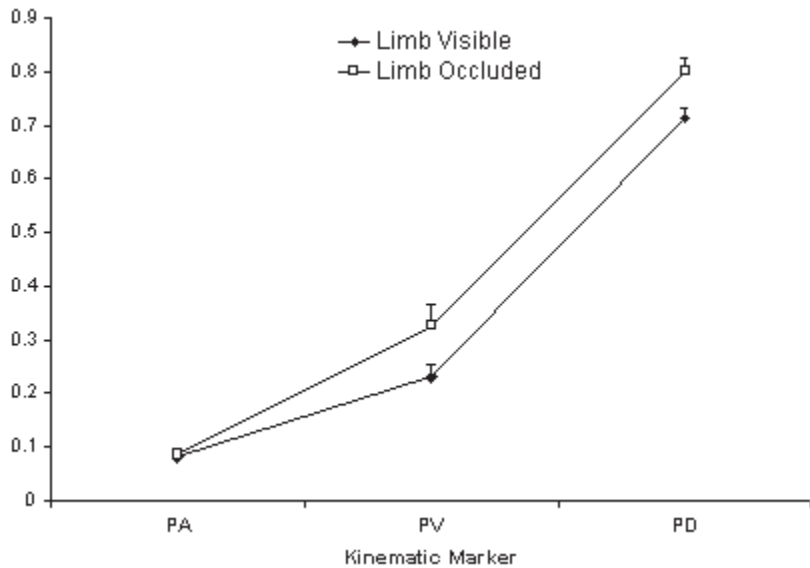
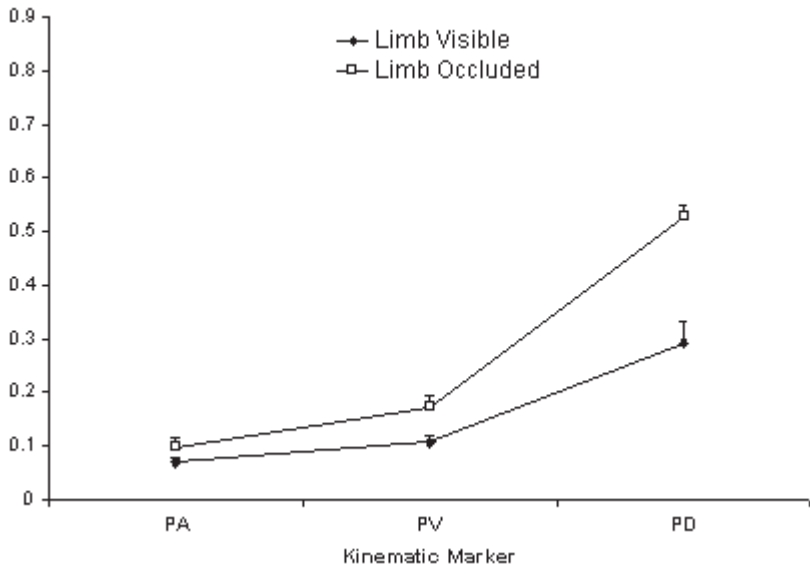


Figure 4—Mean proportion of variance (R²) in movement endpoints explained by the position of the limb at three kinematic markers (PA = peak acceleration, PV = peak velocity, PD = peak deceleration) as a function of limb vision in the primary (top panel) and secondary (bottom panel) movement directions. Error bars represent SEM.

At the outset, the discrepant endpoint characteristics outlined above might be explained by the fact that greater initial force specification resulted in the less accurate and more variable performance of limb occluded trials given that movement times in this condition were significantly faster than their limb visible counterparts (Fitts, 1954; Schmidt et al., 1979). This idea, however, is tempered by the fact that the peak velocities of limb visible (1578 ± 112 mm/s) and limb occluded (1550 ± 106 mm/s) trials did not differ from one another. Instead, the bulk of the kinematic findings (see below) suggest that contrasting control strategies (i.e., offline versus online) contributed to the different endpoint and movement time characteristics.

The claim that limb visible and limb occluded trials were subserved by very different modes of reaching control is supported by three lines of evidence. First, only limb occluded trials significantly undershot the target in the primary movement direction. This result has been linked to a central planning strategy wherein the performer intentionally specifies their movement endpoint to fall short of the actual target location to ensure the mechanical and psychophysical efficiency of the response (Engelbrecht, Berthier, O'Sullivan, 2003; Mendoza & Heath, in press; Worringham, 1991; for recent review see Elliott et al., 2004). Second, participants spent more time after PV during limb visible than limb occluded trials: a finding linked to enhanced accuracy via the evocation of time-consuming discrete (Carlton, 1979; Chua & Elliott, 1993; Meyer et al., 1988) or continuous (Bédard & Proteau, 2004; Beggs & Howarth, 1970; Elliott, Carson, Goodman, & Chua, 1991; Georgopolous, Kalaska, Caminiti, & Massey, 1983; Khan, Elliott, Coull, Chua, & Lyons, 2002) feedback-based movement corrections. Third, the results of the regression analyses showed that limb visible trials yielded only a small to moderate within-trial correspondence between the spatial location of the limb at PA, PV, and PD relative to the ultimate movement endpoint. This pattern of spatial correlations suggests that vision of the moving limb resulted in an online and feedback-based mode of reaching control. Notably, this mode of control enabled participants to detect and correct errors in their reaching trajectory as indexed by the patent accuracy of limb visible trials. Limb occluded trials, however, exhibited more robust within-trial correspondence at the later occurring kinematic landmarks (i.e., PV and PD) suggesting that the pattern and magnitude of endpoint errors in this condition were largely dependent on central planning mechanisms operating in advance of response execution (c.f., Binsted & Heath, 2004; Heath et al., 2004b; Vindras et al., 1998). In other words, the absence of dynamic limb vision resulted in a primarily offline mode of reaching control that did not allow for online attenuation of distance or direction specification errors (Adamovich et al., 1994, 1998; Messier & Kalaska, 1997; Rosenbaum, 1980).

A general issue arising from the regression analyses requires redress: Why did the spatial location of the limb at PA not reliably differentiate between the limb visible and the limb occluded trials? A plausible account for this finding is that PA occurred before the spatiotemporal pattern underlying the initial reaching impulse had sufficient time to unfold. In support of this view, the timing of PA—which was achieved on average 80 ms into limb visible and 82 ms into limb occluded trials—did not reliably differentiate between the two target locations; a finding echoed in other research (e.g., Binsted & Heath, 2004; Heath et al., 2004b;

Messier & Kalaska, 1999, but see Gordon, Ghilardi, & Ghez, 1994). In contrast, the timing of a later occurring kinematic landmark (i.e., PV) elicited a reliable target effect. In addition, it was found that the deceleration phase of limb visible trials was greater than limb occluded trials, thus suggesting that a majority of online control was evoked during the later stage of the reaching trajectory (c.f., Glover, 2004). Consequently, I am led to conclude that the spatial location of the limb at PA did not contain sufficient information to infer the unfolding control strategy associated with the discrete reaching movements studied here.

In sum, the finding that limb visible trials were more accurate and less variable than limb occluded trials compliments some studies arguing that visual input from the moving limb is paramount to maintaining accuracy while reaching to a static target in peripersonal space (e.g., Adamovich, et al., 1998; Carlton, 1981; McIntyre et al., 1998; Zelaznik et al., 1983, but see Elliott, 1988; Foley, 1975; Jeannerod, 1984). Importantly, I was able to link the heightened accuracy of limb visible trials to the evocation of a more online, feedback-based mode of reaching control. Indeed, the intensified error of limb occluded trials appears related to fact that early specification errors went unchecked by the motor system and continued to build until the end of the response.

The Influence of Target Delays on Reaching Accuracy and Control

Recall that the central goals of this investigation were to: (a) test Elliott and Madalena's (1987) hypothesis that a stored sensory (specifically visual) target representation sustains a "highly accurate" online mode of reaching control, and (b) test Glover's (2004) corollary expectation of an inverse relation between the length of visual delay and the extent to which reaches are controlled online. Specifically, Glover proposed that delays greater than 2000 ms affect complete loss of stored target information, resulting in reaches planned wholly in advance of the response (i.e., offline control). Hence, in the following sections I discuss how increasing delays of target information influenced reaching accuracy and control separately for the limb occluded and the limb visible trials studied here.

Limb Occluded Trials and the Manipulation of Visual Target Information.

Providing vision of the target throughout the response (T-V), withdrawing target vision at response onset (T-OL), or withdrawing target vision for 0, 500, 1,500 or 2,500 ms prior to the response (TD-0, TD-500, TD-1500; TD-2500) did not influence the endpoint characteristics of limb occluded trials. In other words, the absence of dynamic limb information produced similar target undershooting in the primary movement direction and similar endpoint error in the secondary movement direction regardless of whether the target was visible during the response or withdrawn for up to 2,500 ms prior to the response. This represents a surprising finding because previous work proposed that increasing delays of target vision lead to increased movement error via the decay of stored target information. For instance, Westwood et al. (2003) reported that target undershooting increased across visual target delays of 0, 500, and 2,000 ms (see also Elliott, 1988; Elliott et al., 1990; Heath & Westwood, 2003; Sheth & Shimojo, 2001; Westwood et al., 2001). Similarly, Heath et al. (2004b) reported a monotonic rise in endpoint variability

with visual target delays of 0, 200, 400, and 600 ms. Thus, a pertinent question to be addressed is why a time-sensitive increase in endpoint error and variability was not observed over the 2,500 ms of target delay used here.

As mentioned earlier, previous work probing the consequence of increased delays on reaching accuracy occluded limb and target vision concurrently by asking participants to close their eyes (e.g., Vince, 1948), turning off the rooms lights (e.g., Elliott et al., 1999b; Elliott & Madalena, 1987) or through the use of visual occlusion devices (e.g., Darling & Miller, 1993; Heath et al., 2004b; Westwood et al., 2000, 2001, 2003). Given those manipulations, the putative contributions of visual limb and visual target delays could not be disentangled because both were removed during the delay interval. Certainly, however, separating the involvement of each represents an important consideration in light of Prablanc and colleagues (e.g., Prablanc et al., 1979) seminal observation that “seeing” one’s limb prior to a response results in reaches that are more accurate and less variable (Desmurget et al., 1995) than when vision of the limb is withdrawn prior to the response. Moreover, endpoint error has been shown to be amplified when premovement delays of visual limb information are increased (Hoehnerman & Levy, 2000), suggesting the fidelity of initial limb coordinate estimation is susceptible to time-sensitive decay processes (Messier, Adamovich, Berkinblit, Tunik, & Poizner, 2003; Rossetti et al., 1994; Vindras et al., 1998).

In the present investigation, the influence of a visual delay of limb information was removed from the effect of increasing delays of visual target information by providing premovement limb information in each target condition. Hence, participants were always able to plan their reaching movement based on visual limb information. As outlined above, this manipulation produced comparable reaching accuracy and variability across target conditions. Specifically, providing participants with vision of the target during the response (T-V trials) resulted in the same endpoint characteristics as observed when vision of the target was withdrawn at movement onset (T-OL) or 0, 500, 1,500 or 2,500 ms prior to the response (see also Elliott & Madalena’s 1987 fast movement time condition). This is a notable finding because it suggests that the time-sensitive decay in reaching accuracy reported in earlier studies using similarly brief delays (i.e., < 2,500 ms: e.g., Elliott et al., 1990; Heath et al., 2004b; Westwood et al., 2001, 2003) might not be attributed to a gradual decay of stored target information. Instead, the present results suggest that decreased initial limb coordinate estimation contributed to the time-sensitive and memory-linked increase in endpoint error reported in earlier work.

Concerning the hypothesis that a highly accurate stored sensory representation of target location is used for online reaching control (Elliott & Madalena, 1987), and the expectation that this representation decays over 2,000 ms of target delay (Glover, 2004), results showed that in each target condition, limb occluded trials exhibited robust R^2 values at the later occurring kinematic markers (i.e., PV and PD). That is, the presence or absence of visual target information—as well as delays of that information—did not influence the fact that the accuracy of limb occluded trials was largely determined by central planning mechanisms. Hence, visual (i.e., T-V trials) as well as stored target information (i.e., T-OL, TD-0, TD-500, TD-1500, TD-2500 trials) was not extensively (if at all) used to support an online mode of

reaching control. Of course, the fact that a primarily offline mode of reaching control was adopted even when the target was visible (i.e., T-V trials) raises the issue of whether the absence of dynamic limb information precluded online control. After all, it is well known that situations affording visual comparisons between limb and target permit metrically precise online movement corrections (see Elliott et al., 2001 for review). Thus, it is entirely possible that the absence of ego-motion cues (i.e., the moving limb) prevented the use of visual or stored target information for online corrections. In a subsequent section, I will return to the important issue of ego-motion cues for the online control of visually guided, open-loop and memory-guided reaches (see "Limb Vision and Online Control," below).

Because it has been established that limb occluded trials demonstrated a primarily offline mode of control, a final issue to be (re)addressed is the nature of information stored in memory and used to plan TD-0 through TD-2500 trials. Certainly stored target information was unnecessary for planning T-V and T-OL trials because vision of the target and the limb was available at response planning, thus providing participants with metrically precise visual limb and visual target information for real time movement specification (Westwood & Goodale, 2003). For the delayed target paradigms, however, stored information was required for movement planning because vision of the target was not available at the time of response cueing. One possibility is that a movement plan based on visual limb and visual target information was generated during the preview and simply held in memory during the delay for later movement execution. A second possibility, and one advocated at the beginning of this article and in the majority of the memory-guided reaching literature (Bridgeman, Lewis, Heit, & Nagle, 1979; Elliott, 1988; Elliott & Madalena, 1987; Glover & Dixon, 2001; Glover, 2004; Haffenden & Goodale, 1998; Heath & Westwood, 2003; Heath et al., 2004a; Hu et al., 2000; McIntyre et al., 1997; Westwood et al., 2000; 2001, 2003), is that a stored sensory representation of the target was constructed during the preview phase and retained in memory until real time conversion into a motor plan (i.e., at the time of response cueing). Although the present study cannot disentangle the two alternatives, two key pieces of evidence are presented to support the latter view.

First, Henry and Rogers (1960) classic work reporting increased reaction time as a function of movement duration and complexity, as well as Klapp's (1975) finding that reaction time can increase in relation to the spatial demands of an upcoming response, argues that the internal structure of a motor plan is specified at the time of response cueing and not before. In other words, the constituent elements of a motor plan are assembled in real time because it is possible that the position of the performer or environmental goal (e.g., location of a target object) can change on a moment-to-moment basis. Thus, a stored sensory representation provides the performer with the greatest level of movement adaptability. Second, evidence from the visual illusions literature indicates that reaching and grasping movements executed after a period of visual delay are more sensitive to the context-dependent properties of visual illusions than are visually guided actions (e.g., Bridgeman et al., 2000; Elliott & Lee, 1995; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Hu et al., 1999; Hu & Goodale, 2000; Westwood et al., 2000). Presumably, visual illusions influence the planning of memory-guided actions to a larger degree than

visually guided responses because the motor system cannot separate the context-dependent properties of the sensory-based target representation retained in memory from the ensuing motor output.

In brief, limb occluded trials elicited a primarily offline mode of reaching control. I therefore conclude that the absence of dynamic limb information provided limited empirical basis to test the hypothesis that stored target information can be used to support an online, feedback-based mode of reaching control. Interestingly, however, because the accuracy of limb occluded trials was not influenced by the different target delays used here, it appears that stored target information can provide a valid and temporally stable substitute for visual target information in terms of serving as a point of reference for movement planning processes.

Limb Visible Trials and the Manipulation of Visual Target Information.

When the limb was visible throughout a response, T-V trials were more accurate than T-OL through TD-2500 trials (which did not differ from one another).⁴ The fact that T-V trials were most accurate is consistent with a large body of research (e.g., Carlton, 1981; Ghez, Gordon, & Ghilardi, 1995b; Meyer et al., 1988; Proteau, Marteniuk, & Levesque, 1992; Woodworth, 1899; Zelaznik et al., 1983), and indirectly supports the view that continuous visual input from limb and target permits metrically precise online limb adjustments. The regression analyses compliment this view in that T-V trials yielded weak R^2 values relating the spatial location of the limb at PA, PV, and PD to the ultimate movement endpoint. In other words, the endpoints of T-V trials were not fully specified at the time of response; rather, online corrections were undertaken to obtain the heightened level of accuracy observed in this condition. Interestingly, and in spite of the fact that visual target information was withdrawn during the execution of T-OL through TD-2500 trials, the R^2 values associated with these conditions indicated a mode of online control on par to that of T-V trials—albeit with less spatial precision (see Figures 1 and 4).

The feedback-based mode of reaching control observed during T-OL through TD-2500 is generally congruent with Elliott and Madalena's (1987) and Glover's (2004) hypothesis that stored target information can be used for online movement corrections. The present results, however, depart from Elliott and Madalena and Glover in terms of the precision and temporal durability afforded by this information source. Concerning the precision of stored target information, Elliott and Madalena's assertion that stored target information provides a "highly accurate" substitute for direct target vision given a delay of less than 2,000 ms (c.f., Elliott, 1988) was not supported by the present work. Although stored target information provided a reasonably accurate source of information for online corrections, it is important to note that reaches in this environment were less accurate than when continuous visual input from the target was available (i.e., T-V trials). Thus, and counter to Elliott and Madalena's influential hypothesis, it appears that there is not a brief window of time in which stored target information provides an equivalent substitute for direct target vision in the implementation of online limb adjustments. Indeed, it is far more likely that stored information provides the motor system a

⁴Recall that T-V trials performed in the limb visible condition represents the only condition in which precise endpoint knowledge of results was available to participants.

reasonable approximation of the target's coordinates in peripersonal space (see also Elliott et al., 1990; Heath & Westwood, 2003; Heath et al., 2004b; Westwood et al., 2001, 2003).

Concerning the temporal durability of stored target information, Glover (2004) proposed that the degree reaches are controlled online diminishes over 2,000 ms of delay. If that prediction were correct, then the correspondence between the location of the limb at any point in the reaching trajectory and the ultimate movement endpoint (i.e., R^2 values) should have been amplified in relation to the length of the target delay. Moreover, TD-2500 reaches should have elicited R^2 values on par to that of limb occluded trials (i.e., limb visible reaches in the TD-2500 condition should have exhibited the offline mode of control characterizing limb occluded trials). Such a prediction is in line with Glover's proposal that delays greater than 2,000 ms result in a complete loss of stored target information for online corrections. As shown in Figures 3 and 4, however, Glover's hypothesis was not borne out: limb visible trials elicited low R^2 values across the target paradigms used here. Indeed, the degree that T-OL through TD-2500 trials were controlled online did not differ from the T-V trials. Hence, there is no evidence to suggest that a brief delay of visual target information (i.e., < 2,500 ms) can influence the degree that reaches are controlled online. On the contrary, the present findings argue that stored target information provides the motor system a temporally durable representation to implement online movement corrections.

That stored target information provided a reasonably accurate, temporally durable representation for online reaching control is matching with the view that memory-based target information is subserved by a visual system quite different from that supporting actions to a visible target (e.g., Milner & Goodale, 1995, see also Berkinblit et al., 1995). First, the patent accuracy of T-V trials is in keeping with the functional properties of the dorsal visual pathway: a visual stream providing the motor system with up-to-date visual limb and visual target information for absolute and online movement corrections (Goodale, Jakobson, & Keillor, 1994; Westwood & Goodale, 2003). Due to the real time nature of the dorsal visual pathway, precise information about the target's coordinates was probably available to the motor system only on a moment-to-moment basis. Thus, it might be the case that the stored target information used for the online control of T-OL through TD-2500 trials was assembled and maintained by perception-based mechanisms residing in the ventral visual pathway. The view that the ventral visual pathway builds and maintains a relative—or cognitive—representation of the visual world is supported by behavioral evidence demonstrating that memory-guided actions are more influenced by the contextual features surrounding a target than are visually guided actions (Hu & Goodale, 2000; Gentilucci et al., 1996; Heath et al., 2004; Heath et al., 2005; Krigolson & Heath, 2004; Westwood et al., 2000; see Milner & Goodale, 1995; see also Goodale & Westwood, 2004, for recent review). Moreover, the fact that neither the accuracy nor the degree that T-OL through TD-2500 trials were controlled online changed over the 2,500 ms of delay used here corresponds with a number of studies arguing that perception-based information affords a long-lasting and stable resource for object-directed actions (Kunde, 2004; Price, Moore, Humphreys, Frackowiak, & Friston, 1996; van Turennout, Bielowicz, &

Martin, 2003). In other words, although the ventral stream offers the motor system a less accurate target representation, it can provide a long-lived spatial referent to support offline (see “Limb Occluded Trials and the Manipulation of Visual Target Information”) and online control processes.

Limb Vision and Online Control

Recall that regardless of visual input from the target, limb visible trials were controlled primarily online, whereas limb occluded trials were regulated primarily offline. Standing on their own, the present results suggest that dynamic (i.e., continuous) limb vision is tantamount to engaging a visual or a stored target representation for online limb adjustments when reaching to a static target presented in an otherwise neutral visual background (Carlton, 1981; see Carlton, 1992, for review). I would, however, like to add that dynamic extrapersonal visual cues might also provide the requisite sensory input to engage online control mechanisms. Indeed, Whitney, Westwood, and Goodale (2003) reported that a vertically drifting background (i.e., a distant motion signal) produced continuous updating of reaching movements to a stationary target. In addition, a considerable literature has shown that a sudden and unexpected perturbation of target location (i.e., a dynamic visual cue) elicits “automatic” limb compensations that are observed whether the limb is visible or occluded during the response (Fecteau, Chua, Franks, & Enns, 2001; Goodale, Pelisson, & Prablanc, 1986; Pisella, Grea, Tilikete et al., 2000). The implication is that any form of dynamic information from the reaching environment—whether limb or target position, or a moving visual background—might represent the requisite sensory input to induce an online mode of reaching control.

Conclusions

In the absence of dynamic limb information, stored target information was not used for online limb adjustments. In contrast, providing participants with vision of their moving limb resulted in the use of a stored target representation for online reaching control. Interestingly, and counter to a recent proposal, the degree reaches were controlled online did not vary over the 2,500 ms of delay used here. I therefore propose that when paired with visual limb information, a stored target representation can provide a reasonably accurate and temporally stable referent for executing error-nullifying movement corrections given a sufficiently brief target delay (< 2,500 ms).

References

- Abrams, R.A., & Pratt, J. (1993). Rapid aimed limb movements: Differential effects of practice on component submovements. *Journal of Motor Behavior*, 25, 288-298.
- Adamovich, S.V., Berkinblit, M.B., Fookson, O., & Poizner, H. (1998). Pointing in 3D space to remembered targets. 1. Kinesthetic versus visual target presentation. *Journal of Neurophysiology*, 79, 2833-2846.
- Adamovich, S.V., Berkinblit, M.B., Smetanin, B., Fookson, O., & Poizner, H. (1994). Influence of movement speed on accuracy of pointing to memorized targets in 3D space. *Neuroscience Letters*, 172, 171-174.

- Bédard, P., & Proteau, L. (2004). On-line vs. off-line utilization of peripheral visual afferent information to ensure spatial accuracy of goal-directed movements. *Experimental Brain Research*, 158, 75-85.
- Beggs, W.D.A., & Howarth, C.L. (1970). Movement control in a repetitive task. *Nature*, 225, 752-753.
- Berkinblit, M.B., Fookson, O.I., Smetanin, B., Adamovich S.V., & Poizner, H. (1995). The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. *Experimental Brain Research*, 107, 326-330.
- Binsted, G., & Heath, M. (2004). Can the motor system utilize a stored representation to control movement? A commentary on Glover. *Behavioral Brain Sciences*, 27, 25-27.
- Binsted, G., & Heath, M. (2005). No evidence of a lower field specialization for visuo-motor control. *Experimental Brain Research*, 162, 89-94.
- Bridgeman, B., Gemmer, A., Forsman, T., & Huemer, V. (2000). Processing spatial information in the sensorimotor branch of the visual system. *Vision Research*, 40, 3539-3553.
- Bridgeman, B., Lewis, S., Heit, G., & Nagle, M. (1979). Relation between cognitive and motor-oriented systems of visual position perception. *Journal of Experimental Psychology: Human Perception and Performance*, 5, 692-700.
- Bryden, M.P. (1977). Measuring handedness with questionnaires. *Neuropsychologia*, 15, 617-624.
- Carlton, L.G. (1979). Control processes in the production of discrete aiming responses. *Journal of Human Movement Studies*, 5, 115-124.
- Carlton, L.G. (1981). Visual information: The control of aiming movements. *Quarterly Journal of Experimental Psychology*, 33A, 87-93.
- Carlton, L.G. (1992). Visual processing time and the control of movement. In L. Proteau & D. Elliott (Eds.), *Vision and motor control* (pp. 3-31). Amsterdam: North Holland.
- Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Human Movement Science*, 12, 365-401.
- Churchill, A., Hopkins, B., Ronqvist, L., & Vogt, S. (2000). Vision of the hand and environmental context in human prehension. *Experimental Brain Research*, 134, 81-89.
- Darling, W.G., & Miller, G.F. (1993). Transformation between visual and kinesthetic coordinate systems in reaches to remembered object locations and orientations. *Experimental Brain Research*, 93, 534-547.
- Desmurget, M., Rossetti, Y., Jordan, M., Meckler, C., & Prablanc, C. (1997). Viewing the hand prior to movement improves accuracy of pointing performed toward the unseen contralateral hand. *Experimental Brain Research*, 115, 180-186.
- Desmurget, M., Rossetti, Y., Prablanc, C., Stelmach, G.E., & Jeannerod, M. (1995). Representation of hand position prior to movement and motor variability. *Canadian Journal of Physiology and Pharmacology*, 73, 262-272.
- Elliott, D. (1988). The influence of visual target and limb information on manual aiming. *Canadian Journal of Psychology*, 42, 57-68.
- Elliott, D., & Binsted, G., Heath, M. (1999a). The control of goal-directed limb movements: Correcting errors in the trajectory. *Human Movement Science*, 18, 121-136.
- Elliott, D., Calvert, R., Jaeger, M., & Jones, R. (1990). A visual representation and the control of manual aiming movements. *Journal of Motor Behavior*, 22, 327-346.

- Elliott, D., Carson, R.G., Goodman, D., & Chua, R. (1991). Discrete vs. continuous control of manual aiming. *Human Movement Science*, 10, 393-418.
- Elliott, D., Hansen, S., Mendoza, J., & Tremblay, T. (2004). Learning to optimize speed, accuracy and energy expenditure: A framework for understanding speed-accuracy relations in goal-directed aiming. *Journal of Motor Behavior*, 36, 339-351.
- Elliott, D., Heath, M., Binsted, G., Ricker, K.L., Roy, E.A., & Chua, R. (1999b). Goal-directed aiming: Correcting a force specification error with the right and left hands. *Journal of Motor Behavior*, 31, 309-324.
- Elliott, D., Helsen, W.F., & Chua, R. (2001). A century later: Woodworth's (1899) two-component model of goal-directed aiming. *Psychological Bulletin*, 127, 342-357.
- Elliott, D., & Lee, T.D. (1995). The role of target information on manual-aiming bias. *Psychological Research*, 58, 2-9.
- Elliott, D., Lyons, J., Chua, R., Goodman, D., & Carson, R. G. (1995). The influence of target perturbation on manual aiming asymmetries in right handers. *Cortex*, 31, 985-997.
- Elliott, D., & Madalena, J. (1987). The influence of premovement visual information on manual aiming. *Quarterly Journal of Experimental Psychology*, 39A, 541-559.
- Engelbrecht, S. E., Berthier, N. E., & O'Sullivan, L. (2003). The undershooting bias: Learning to act optimally under uncertainty. *Psychological Research*, 14, 257-261.
- Fecteau, J.H., Chua, R., Franks, I., & Enns, J.T. (2001). Visual awareness and the online modification of action. *Canadian Journal of Experimental Psychology*, 55, 104-110.
- Fitts, P.M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 47, 381-391.
- Foley, J.M. (1975). Error in visually directed manual pointing. *Perception and Psychophysics*, 17, 69-74.
- Gentilucci, M., Chieffi, S., Daprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologia*, 34, 369-376.
- Georgopoulos, A.P., Kalaska, J.F., Caminiti, R., & Massey, J.T. (1983). Interruption of motor cortical discharge subserving aimed arm movements. *Experimental Brain Research*, 49, 327-340.
- Ghez, C., Gordon, J., & Ghilardi, M.F. (1995a). Impairments of reaching movement in patients without proprioception. I. Spatial errors. *Journal of Neurophysiology*, 73, 347-360.
- Ghez, C., Gordon, J., & Ghilardi, M.F. (1995b). Contributions of vision and proprioception to accuracy in limb movements. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 549-664). Cambridge, MA: MIT Press.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *Behavioral and Brain Sciences*, 27, 3-78.
- Glover, S., & Dixon, P. (2001). Motor adaptation to an optical illusion. *Experimental Brain Research*, 137, 254-258.
- Goodale, M.A., Jakobson, L.S., & Keillor, J.M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, 32, 1159-1178.
- Goodale, M.A., Pelisson, D., & Prablanc, D. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature*, 320, 748-750.

- Goodale, M.A., & Westwood, D.A. (2004). An evolving view of duplex vision: separate but interacting cortical visual pathways for perception and action. *Current Opinions in Neurobiology*, 14, 203-211.
- Gordon, J., Ghilardi, M.F., & Ghez, C. (1994). Accuracy of planar reaching movements. I. Independence of direction and extent variability. *Experimental Brain Research*, 99, 97-111.
- Haffenden, A.M., & Goodale, M.A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience*, 10, 122-136.
- Heath, M., Hodges, N.J., Chua, R., & Elliott, D. (1998). On-line control of rapid aiming movements: Unexpected target perturbations and movement kinematics. *Canadian Journal of Experimental Psychology*, 52, 163-173.
- Heath, M., & Rival, C. (2005). Role of the visuomotor system in on-line attenuation of a pre-movement illusory bias in grip aperture. *Brain and Cognition*, 57(2), 111-114.
- Heath, M., Rival, C., & Binsted, G. (2004a). Can the motor system resolve a pre-movement bias in grip aperture: Online analysis of grasping the Müller-Lyer illusion. *Experimental Brain Research*, 158, 378-384.
- Heath, M., Rival, C., Westwood, D.A. & Neely, K. (in press). Time course analysis of closed- and open-loop grasping of the Müller-Lyer illusion. *Journal of Motor Behavior*.
- Heath, M., & Westwood, D.A. (2003). Can a visual representation support the online control of memory-dependent aiming? Evidence from a variable spatial mapping paradigm. *Motor Control*, 7, 346-361.
- Heath, M., Westwood, D.A., & Binsted, G. (2004b). The control of memory-guided reaching movements in peripersonal space. *Motor Control*, 8, 76-106.
- Held, R., & Gottlieb N. (1958). Technique for studying adaptation to disarranged hand-eye coordination. *Perceptual and Motor Skills*, 8, 83-86.
- Henry, F.M., & Rogers, D.E. (1960). Increased response latency for complication movements and a "memory drum" theory of neuromotor reaction. *Research Quarterly for Exercise and Sport*, 31, 448-458.
- Hocherman, S., & Levy, H. (2000). The role of feedback in manual tracking of visual targets. *Perceptual and Motor Skills*, 90, 1234-1248.
- Hu, Y., Eagleson, R., & Goodale, M.A. (1999). The effects of delay on the kinematics of grasping. *Experimental Brain Research*, 126, 109-116.
- Hu, Y., & Goodale, M.A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics. *Journal of Cognitive Neuroscience*, 12, 856-868.
- Jeannerod, M. (1984). The timing of natural prehension movements. *Journal of Motor Behavior*, 16, 235-254.
- Jeannerod, M. (1986). Mechanisms of visuomotor coordination: A study in normal and brain-damaged subjects. *Neuropsychologia*, 24, 41-78.
- Khan, M.A., Elliott, D., Coull, J., Chua, R., & Lyons, J. (2002). Optimal control strategies under different feedback schedules: Kinematic evidence. *Journal of Motor Behavior*, 34, 45-57.
- Khan, M.A., & Franks, I.M. (2000). The effect of practice on component submovements is dependent on visual feedback. *Journal of Motor Behavior*, 32, 227-240.
- Keele, S.W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, 70, 387-403.

- Klapp, S.T. (1975). Feedback versus motor programming in the control of aimed movements. *Journal of Experimental Psychology: Human Perception and Performance*, 1, 147-153.
- Krigolson, O., & Heath, M. (2004). Background visual cues and memory-guided reaches. *Human Movement Science*, 23, 861-877.
- Kunde, W. (2004). Response priming by supraliminal and subliminal action effects. *Psychological Research*, 68, 91-96.
- Langolf, G.D., Chaffin, D.B., & Foulke, J.A. (1976). An investigation of Fitts' law using a wide range of movement amplitudes. *Journal of Motor Behavior*, 8, 113-128.
- Lemay, M., & Proteau, L. (2001). A distance effect in a manual aiming task to remembered targets: A test of three hypothesis. *Experimental Brain Research*, 140, 357-368.
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology*, 78, 1601-1618.
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: Psychophysical evidence for body-centered reference frames. *Journal of Neuroscience*, 18, 8423-8435.
- Mendoza, M., & Heath, M. (in press). Reaching in near and far peripersonal space: No evidence for contrasting control strategies. *Journal of Sport and Exercise Psychology*.
- Messier, J., Adamovich, S., Berkinblit, M., Tunik, E., & Poizner, H. (2003). Influence of movement speed on accuracy and coordination of reaching movements to memorized targets in three-dimensional space in a deafferented subject. *Experimental Brain Research*, 150, 399-416.
- Messier, J., & Kalaska, J.F. (1997). Differential effect of task conditions on errors of direction and extent of reaching movements. *Experimental Brain Research*, 115, 469-478.
- Messier, J., & Kalaska, J.F. (1999). Comparison of variability of initial kinematics and endpoints of reaching movements. *Experimental Brain Research*, 125, 139-152.
- Meyer, D.A., Abrams, R.A., Kornblum, S., Wright, C.E., & Smith, J.E.K. (1988). Optimality in human motor performance: Ideal control of rapid aimed movements. *Psychological Review*, 95, 340-370.
- Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action*. Oxford: University Press.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D., & Rossetti, Y. (2000). An 'automatic pilot' for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, 3, 729-736.
- Plamondon, R. (1995). A kinematic theory of rapid human movements. Part I. Movement representation and generation. *Biological Cybernetics*, 72, 295-307.
- Prablanc, C., Echallier, J.E., Jeannerod, M., & Komilis, E. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. II. Static and dynamic visual cues in the control of hand movement. *Biological Cybernetics*, 35, 183-187.
- Pratt, J., & Abrams, R.A. (1996). Practice and component submovements: The roles of programming and feedback in rapid aimed limb movements. *Journal of Motor Behavior*, 28, 149-156.
- Previc, F.H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, 124, 123-164.

- Price, C.J., Moore, C.J., Humphreys, G.W., Frackowiak, R.S., & Friston, K.J. (1996). The neural regions sustaining object recognition and naming. *Proceedings from the Royal Society of London: Biological Sciences*, 22, 1501-1507.
- Proteau, L., & Cournoyer, J. (1990). Vision of the stylus in a manual aiming task. The effects of practice. *Quarterly Journal of Experimental Psychology*, 42B, 811-828.
- Proteau, L., Marteniuk, R.G., & Levesque, L. (1992). A sensorimotor basis for motor learning: Evidence indicating specificity of practice. *Quarterly Journal of Experimental Psychology*, 44A, 557-575.
- Redon, C., Hay, L., & Velay, J.L. (1991). Proprioceptive control of goal-directed movements in man, studied by means of vibratory muscle tendon stimulation. *Journal of Motor Behavior*, 23, 101-108.
- Rosenbaum, D.A. (1980). Human movement initiation: specification of arm, direction, and extent. *Journal of Experimental Psychology: General*, 109, 444-474.
- Rossetti, Y., Stelmach, G., Desmurget, M., Prablanc, C., & Jeannerod, M. (1994). The effect of viewing the static hand prior to movement onset on pointing kinematics and variability. *Experimental Brain Research*, 101, 323-330.
- Sarlegna, F., Blouin, J., Bresciani, J.P., Bourdin, C., Vercher, J.L., & Gauthier, G.M. (2003). Target and hand position information in the online control of goal-directed arm movements. *Experimental Brain Research*, 151, 524-535.
- Schmidt, R.A., Zelaznik, H.N., Hawkins, B., Frank, J.S., & Quinn, J.T. (1979). Motor-output variability. A theory for the accuracy of rapid acts. *Psychological Review*, 47, 415-451.
- Sheth, B.R., & Shimojo, S. (2001). Compression of space in visual memory. *Vision Research*, 41, 329-341.
- Soechting, J.F. (1984). Effect of target size on spatial and temporal characteristics of pointing movement in man. *Experimental Brain Research*, 54, 121-132.
- van Donkelaar, P., & Franks, I.M. (1991). The effects of changing movement velocity and complexity on response preparation: Evidence from latency, kinematic and EMG measures. *Experimental Brain Research*, 83, 618-623.
- van Turennout, M., Bielamowicz, L., & Martin, A. (2003). Modulation of neural activity during object naming: Effects of time and practice. *Cerebral Cortex*, 13, 381-391.
- Vince, M.A. (1948) Corrective movements in a pursuit task. *Quarterly Journal of Experimental Psychology*, 1, 85-103.
- Vindras, P., Desmurget, M., Prablanc, C., & Viviani, P. (1998). Pointing errors reflect biases in the perception of the initial hand position. *Journal of Neurophysiology*, 79, 3290-3294.
- Westwood, D.A., & Goodale, M.A. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision*, 16, 243-254.
- Westwood, D.A., Heath, M., & Roy, E.A. (2000). The effect of a pictorial illusion on closed-loop and open-loop prehension. *Experimental Brain Research*, 134, 456-463.
- Westwood, D.A., Heath, M., & Roy, E.A. (2001). The accuracy of manual-aiming movements in brief delay conditions. *Canadian Journal of Experimental Psychology*, 55, 304-310.
- Westwood, D.A., Heath, M., & Roy, E.A. (2003). No evidence for accurate visuomotor memory: Systematic and variable error in memory-guided reaching. *Journal of Motor Behavior*, 35, 127-133.

- Whitney, D., Westwood, D.A., & Goodale, M.A. (2003). The influence of visual motion on fast reaching movements to a stationary. *Nature*, 423, 869-873.
- Woodworth, R.S. (1899). The accuracy of voluntary movement. *Psychological Review*, 3, 1-114.
- Worringham, C.J. (1991). Variability effects on the internal structure of rapid aiming movements. *Journal of Motor Behavior*, 23, 75-85.
- Zelaznik, H., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*, 15, 217-236.

Copyright of Motor Control is the property of Human Kinetics Publishers, Inc.. The copyright in an individual article may be maintained by the author in certain cases. Content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.