

The proximity of visual landmarks impacts reaching performance

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Received 16 May 2006; accepted 21 December 2006

Abstract—The control of goal-directed reaching movements is thought to rely upon egocentric visual information derived from the visuomotor networks of the dorsal visual pathway. However, recent research (Krigolson and Heath, 2004) suggests it is also possible to make allocentric comparisons between a visual background and a target object to facilitate reaching accuracy. Here we sought to determine if the effectiveness of these allocentric comparisons is reduced as distance between a visual background and a target object increases. To accomplish this, participants completed memory-guided reaching movements to targets presented in an otherwise empty visual background or positioned within a proximal, medial, or distal visual background. Our results indicated that the availability of a proximal or medial visual background reduced endpoint variability relative to reaches made without a visual background. Interestingly, we found that endpoint variability was not reduced when participants reached to targets framed within a distal visual background. Such findings suggest that allocentric visual information is used to facilitate reaching performance; however, the fidelity by which such cues are used appears linked to the proximity of veridical target location. Importantly, these data also suggest that information from both the dorsal and ventral visual streams can be integrated to facilitate the online control of reaching movements.

Keywords: Reaching; visual background; memory-guided; egocentric; allocentric.

INTRODUCTION

The processing of visual information appears to be dissociable into two distinct visual streams: a dorsal visual stream dedicated to the control of goal-directed reaching movements and a ventral visual stream tasked primarily with perceptual identification (Goodale, 2005; Goodale and Milner, 1992; Goodale and Westwood,

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2004; Goodale *et al.*, 2004; Milner and Goodale, 1995; Obhi and Goodale, 2005; Westwood and Goodale, 2003). The role of the dorsal visual stream in motor control is readily apparent when vision of the movement environment is available. In these instances, it is generally thought that goal-directed actions are mediated using egocentric visual information derived from the dorsal visual stream. In particular, a growing body of imaging, lesion, and trans-cranial magnetic stimulation studies suggest that the dorsal visual stream (specifically posterior parietal cortex) plays an important role in the online control of movement (i.e. Desmurget *et al.*, 1999, 2001; Grea *et al.*, 2002; Pisella *et al.*, 2000). However, when vision of the movement environment is not available (i.e. reaches made to a remembered target object), it is believed that allocentric visual information derived from the ventral visual stream is used to organize and execute reaching movements (Goodale and Humphrey, 1998; Heath *et al.*, 2004a; Hu and Goodale, 2000; Westwood *et al.*, 2003). With that said, there is also experimental evidence which suggests that the dorsal visual stream also plays a role in the planning of memory-guided reaching movements. For instance, Grandt and Andersen (1987) observed activity in the lateral bank of the intraparietal cortex in a Rhesus monkey related to the planning of memory-guided movements.

Although a large number of studies have examined the two visual streams independently, a growing body of evidence suggests that egocentric and allocentric visual information can be used in conjunction to facilitate the planning, execution, and online control of reaching movements. Seminal work by Conti and Beaubaton (1980) and Velay and Beaubaton (1986) first examined this issue in two studies wherein participants reached to targets that were presented in isolation or were embedded within a grid-like pattern. The results of these experiments indicated that endpoint error was reduced on trials when the grid-like pattern was visible. Furthermore, Velay and Beaubaton manipulated the availability of the visual background so that it was: (a) continuously visible throughout a reaching movement; (b) visible only at movement onset; and (c) not visible at all. Interestingly, Velay and Beaubaton's results demonstrated that reaches were more accurate on trials when the visual background was available during the movement. This result suggested that availability of the visual background primarily facilitated online control mechanisms as opposed to movement planning processes. Thus, the work of Beaubaton and colleagues provided evidence that allocentric visual information (i.e. background and target comparisons) is used in combination with egocentric visual information to facilitate reaching accuracy. Furthermore, these data also suggest that the allocentric visual information provided by the availability of a visual background primarily impacts the online control phase of goal-directed actions (as opposed to movement planning and/or the ballistic phase of a reaching movement, Coello and Grealley, 1997; Proteau and Masson, 1997, but see Obhi and Goodale, 2005).

The impact of a visual background on reaching accuracy has also been examined when vision of the target is not available (i.e. memory-guided conditions). Indeed, it appears that the availability of perceived (Carrozzo *et al.*, 2002) or physical landmarks (Barry *et al.*, 1997; Krigolson and Heath, 2004; Lemay *et al.*, 2004;

Obhi and Goodale, 2005; Sheth and Shimojo, 2004) facilitates reaching accuracy to remembered targets. For example, Krigolson and Heath recently examined the impact of a visual background on the planning and control of visually guided and memory-guided reaches. In this experiment, participants reached to a target that was either visible at all times, occluded at movement onset (an open-loop condition), or was occluded 0 or 1000 ms before a movement initiation cue (memory-guided conditions). On one-half of the experimental trials, the target was framed with a visual background; for the remaining trials, the target was presented in isolation. The results of this experiment indicated that endpoints were more accurate and less variable when a visual background was available, independent of visual condition. Furthermore, the results also suggested that when the visual background was available participants engaged online movement control mechanisms to a greater extent than when the visual background was not available. As mentioned above, it is worth noting that there is evidence suggesting that the availability of a visual background also facilitates movement planning processes by stabilizing the target location (Obhi and Goodale, 2005). In sum, the results of the aforementioned studies suggest that when vision of a target is removed, additional allocentric visual information (i.e. a visual background) can be used to facilitate reaching accuracy.

It seems a reasonable assumption that in most manual reaching paradigms there are some extraneous visual cues that could provide a basis for allocentric comparisons. For instance, in studies where only vision of the movement target is occluded, the edge of a computer monitor or table could in theory provide a valid reference point for framing the remembered target location. However, it seems plausible that the allocentric comparisons used to facilitate memory-dependent reaches may only be effective if the visual landmarks used to make the comparison are in close proximity to the remembered location of the target object. As such, an unresolved question relates to whether or not the displacement (i.e. the linear distance) between the object comprising the visual background and the remembered target location impacts the effectiveness, or degree, by which allocentric comparisons are used to support reaching control in memory-dependent conditions. In the present study we addressed this question by having participants perform reaching movements in four memory-dependent conditions (see below) to a target that was either presented in isolation or framed within a proximal, medial, or distal visual background. Importantly, this manipulation varied the displacement of the visual background from the remembered target location. In line with previous research (i.e. Krigolson and Heath, 2004), we hypothesized that a visual background would enhance movement accuracy and stability relative to a situation wherein a target object is presented in an otherwise neutral or empty visual background. However, we also predicted that increased displacement between a visual background cue and a remembered target would result in a decrease in endpoint accuracy and an increase in endpoint variability (i.e. reaches made in the distal visual background condition would be less accurate and more variable than reaches made in the proximal visual background condition).

METHODS

Participants

Fourteen volunteers (18–30 years of age) from the University of Saskatchewan community volunteered to participate in this study. Participants had normal or corrected-to-normal vision and were right-handed by self-report. Informed consent was obtained in accordance with the University of Saskatchewan Advisory Committee on Ethics.

Apparatus

Participants sat 50 cm in front of an inclined surface and completed goal-directed reaching movements in the transverse axis (moving from left to right). The inclined surface was constructed of a translucent plastic to allow a computer data projector (NEC VT-465) to back project visual stimuli onto the reaching surface. All experimental stimuli were presented using EPrime software (PST Inc., version 1.1). Reaching movements were executed from a common home position (a 1 cm diameter red circle, 1.2° of visual angle) presented level with the participants midline and 17 cm to the left of centre. Participants began each trial by depressing a microswitch located at the home position. Reaches were made to two targets located 32 and 35 cm to the right of the home position along the midline transverse axis in four visual conditions (see below). In addition, on some trials four green circles (1 cm diameter, 1.2° of visual angle) were presented in a 6 cm by 6 cm (6.8° of visual angle), 9 cm by 9 cm (10.2° of visual angle), or a 12 cm by 12 cm (13.5° of visual angle) square around the target thus providing participants with a structured visual background (see Fig. 1 for more detail). The presentation and timing of visual information was yoked to a microswitch mounted at the home position. Participants were instructed to keep their eyes on the target location at all times. As we had no reason to believe that there would be eye movement differences associated with the different experimental conditions (see Note 1), we did not record eye movements with tracking equipment in the present experiment. Finally, the experiment was performed in a darkened room to remove extraneous allocentric visual cues.

Procedure

Participants were instructed to complete discrete reaching movements ‘as quickly and accurately as possible’ to the illuminated red target in response to an auditory movement initiation cue. Experimental trials were differentiated into four visual conditions in order to gauge the impact of visual background-remembered target comparisons across an increasing series of memory delays. Within each visual condition, experimental trials were further differentiated into four background displacement conditions and two target displacement conditions. All visual conditions began with a two-second preview period in which the start position, target, and visual

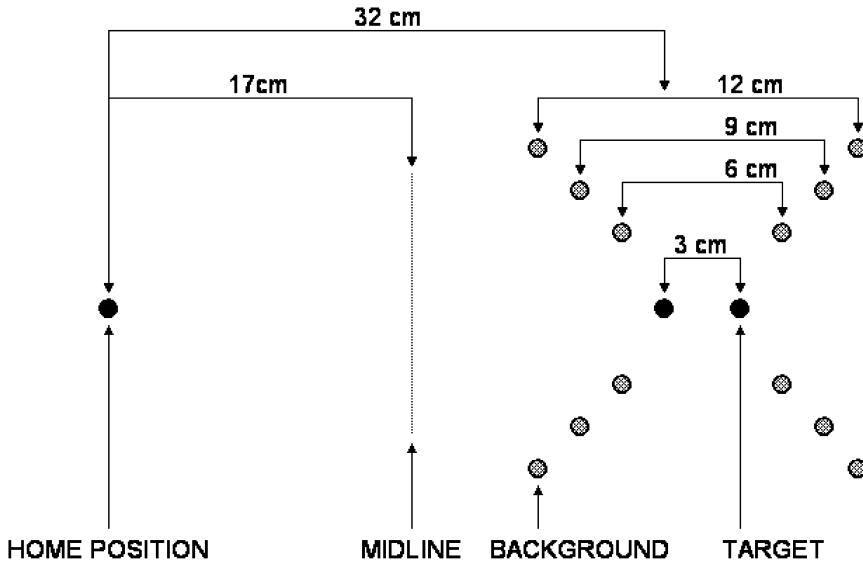


Figure 1. Diagram of visual stimuli. Note that while the midline is pictured for orientation purposes, it was not visible on the aiming surface.

background (when available) were visible. The first visual condition was an open-loop (OL) condition where an auditory initiation cue was presented immediately following the preview phase. In this condition, vision of the target was occluded as soon as participants initiated their reach (i.e. pressure was released from the home position microswitch). Participants also completed reaches in delay conditions of 0, 1000 and 2000 ms (i.e. D0, D1000 and D2000). In the delay conditions, vision of the target was removed immediately following the preview phase, with the auditory initiation tone sounding following a delay of either 0, 1000 or 2000 ms. In all of these conditions, participants retained vision of the reaching environment and their finger throughout the reaching movement.

To assess whether different background displacements impacted reaching accuracy to remembered target locations there were four background conditions factorially arranged within each of the four vision conditions. In the first background condition, no-visual background (NVB), the target was presented against an otherwise empty visual environment. Importantly, in the NVB condition there were no extraneous visual landmarks in the reaching environment thus participants were not able to make allocentric comparisons to facilitate reaching accuracy. As such, the NVB condition provided a viable comparison condition for gauging the impact of a visual background on reaching accuracy. In the other three background conditions (proximal, middle, distal), the target was centrally presented within a square of 1 cm diameter green circles during the preview phase (see above). In these conditions participants were able to make allocentric comparisons between the visual background and the remembered target location to facilitate reaching accuracy. In all background conditions, the background circles remained visible throughout the

reaching movement. Knowledge of results was not explicitly provided to participants; however, participants were able to evaluate their terminal accuracy relative to the visual background when available. Visual (4) and background (4) conditions were organized into 16 randomly ordered trial blocks, with target displacement (2) presented an equal number of times in a pseudo-random fashion. Participants completed 8 reaches in each of these conditions, yielding a total of 256 trials in the present experiment.

Data collection and reduction

A single infra-red emitting diode was affixed to the end of a finger clip worn by participants in order to attain positional information throughout the reaching movement. The position of the infra-red emitting diode was sampled at 250 Hz for 2 s following the auditory initiation tone using a Visualyze 4000 (Phoenix Technologies Inc., Burnaby, British Columbia, Canada). After data collection, the raw displacement data were filtered with a second-order dual-pass Butterworth filter using a low-pass cut-off frequency of 15 Hz (*cf.* Krigolson and Heath, 2004; Winter and Patla, 1997) (see Note 2). Next, we determined instantaneous velocities by differentiating the displacement values using a two-point central finite difference algorithm. Subsequently, we obtained instantaneous acceleration values by differentiating the instantaneous velocity data. Movement onset was identified as the first frame of 10 consecutive frames (50 ms) in which velocity exceeded 50 mm/s. Movement offset was identified as the first frame of 10 consecutive frames (50 ms) in which velocity was less than 50 mm/s.

Dependent variables in the present study included: reaction time (time between the auditory initiation cue and movement onset); movement time (time between movement onset and offset); constant error in the primary (error to the left or right of the target); and secondary (error above or below the target) movement directions and their associated variable error values (i.e. within-participant standard deviation), and peak velocity (maximum resultant velocity between movement onset and offset). We also employed two analysis techniques to examine the use of online control strategies in the different visual and background conditions. Previous research suggests that the proportion of movement time spent after peak velocity is indicative of online motor control — the greater the proportion of movement time spent after peak velocity the greater the use of online control processes (*cf.* Khan *et al.*, 2002). As such, in the present study we computed the proportional time spent after peak velocity for each experimental condition. We also employed a regression analysis to determine the proportion of endpoint variance (R^2) explained by the spatial position of the limb (primary and secondary movement directions) at 25%, 50% and 75% of the reaching trajectory (e.g. Binsted and Heath, 2004; Elliott *et al.*, 1999; Heath, 2005; Heath *et al.*, 2004a; Krigolson and Heath, 2004). The logic behind this technique is that, if participants are engaged in online, feedback-based control, then R^2 values at this point in the reaching trajectory will be lower than if the reaching movement was primarily specified in advance of movement onset. By

comparing the R^2 values for the visual background conditions at 25%, 50% and 75% of the reaching trajectory we sought to determine whether the presence of the visual background facilitated online movement control. Note that we only utilised this analysis in the primary movement direction as in the secondary movement direction we would anticipate high R^2 values both early and late in the reaching trajectory.

All omnibus tests were interpreted using an alpha level of 0.05. Significant effects/interactions requiring *post-hoc* examination were subjected to simple effects analyses and a Bonferroni correction for multiple comparisons ($\alpha < 0.05$). Lowest bound corrections were applied when necessary for violations of the assumption of sphericity. To assist with the interpretation of effect size, partial eta squared (η) or Cohen's d values are reported. Note that all standard deviation statistics were calculated using the within subjects specifications (see Loftus and Masson, 1994).

RESULTS

Performance measures

To examine the effects the visual conditions, background conditions, and target displacements (and the possible interactions) on reaction time, movement time, constant error, and variable error we submitted these data each to a 4 (visual condition: OL, D0, D1000, D2000) by 4 (background condition: NVB, PVB, MVB, DVB) by 2 (target displacement: near, far) fully repeated-measures ANOVAs.

The examination of reaction time yielded an effect for visual condition, $F(3, 39) = 8.20$, $p < 0.001$ [$\eta = 0.39$], such that OL (227 ms [SD 34]) and D0 (221 ms [SD 34]) reaches elicited shorter reaction times than D1000 (267 ms [SD 34]) and D2000 reaches (267 ms [SD 34]) ($p < 0.05$). The movement time analysis revealed main effects for visual condition, $F(3, 39) = 9.34$, $p < 0.001$ [$\eta = 0.42$], and target displacement, $F(1, 13) = 27.89$, $p < 0.001$ [$\eta = 0.68$]. The effect of visual condition indicated that movement time was shorter for OL reaches than for D0, D1000 and D2000 reaches which did not differ ($p < 0.05$) (see Fig. 2, middle panel). The effect for target displacement indicated that movement time increased with increasing target eccentricity (486 ms [SD 10] *versus* 498 ms [SD 10]).

In the primary movement direction the analysis of constant error yielded a main effect for visual condition, $F(3, 39) = 4.52$, $p < 0.01$ [$\eta = 0.42$]: OL reaches were more accurate than D0, D1000 and D2000 reaches ($p < 0.05$) (see Fig. 2, middle panel). The analysis of constant error in the secondary movement direction revealed a main effect for target displacement, $F(1, 13) = 110.32$, $p < 0.001$ [$\eta = 0.89$], indicating reaches to the near target yielded greater upward bias at movement end than reaches to the far target (15 mm [SD 13] *versus* -4 mm [SD 13]). Note that for constant error there was no visual condition by background condition interaction in either movement direction (primary: $F(9, 117) = 1.09$, $p > 0.05$ [$\eta = 0.08$]; secondary: $F(9, 117) = 2.00$, $p > 0.05$ [$\eta = 0.13$]).

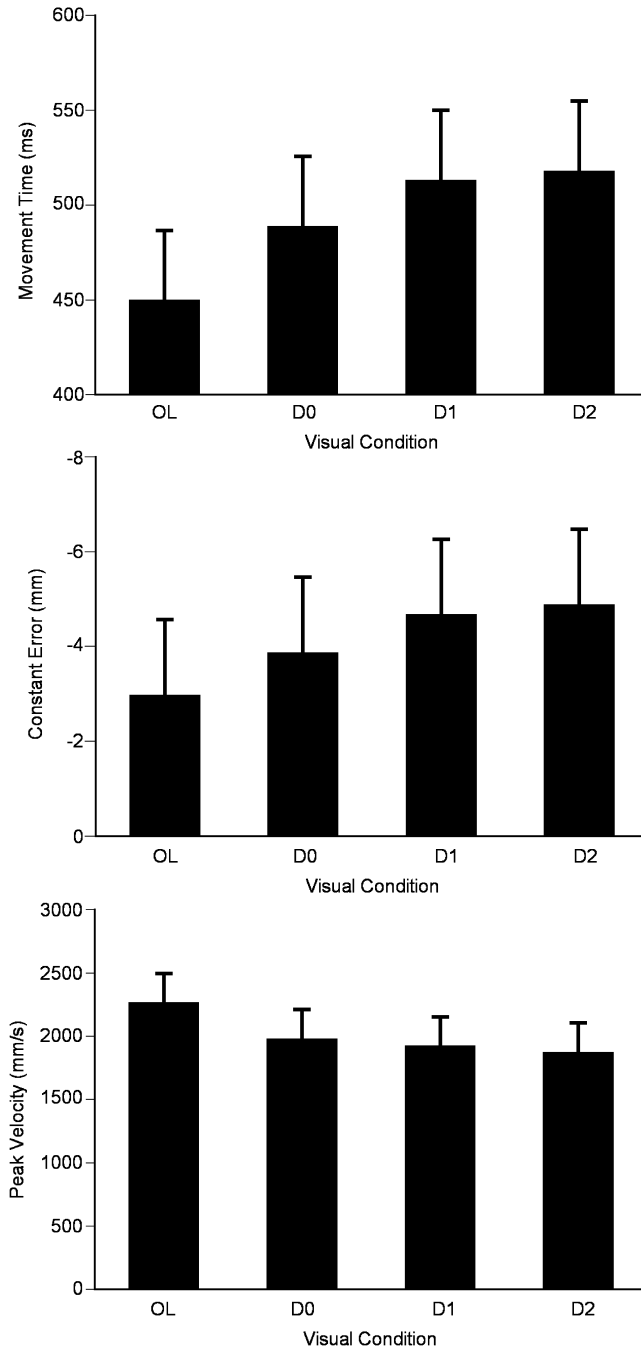


Figure 2. Movement time (ms: top panel), constant error in the primary movement direction (mm: middle panel) and peak velocity (mm/s: bottom panel) as a function of visual condition. Error bars represent within-participant standard deviations.

Analysis of variable error in the primary movement direction revealed a main effect for background condition, $F(3, 39) = 4.73$, $p < 0.01$ [$\eta = 0.27$]. Reaches made in the PVB and MVB conditions were less variable than reaches made in the NVB and DVB conditions ($p < 0.05$) (see Figs 3 and 4). Given our *a priori* hypothesis predicting an increase in variable error in relation to increasing background displacement, we also statistically compared variable error for the PVB and MVB conditions directly. Interestingly, this analysis revealed that variable error was statistically equivalent between these two conditions, $t(14) = 0.67$, $p > 0.05$ [$d = 0.37$]. The analysis of variable error in the secondary movement analysis indicated a main effect for background condition mirroring the effect just described (i.e. for the primary movement direction), $F(3, 39) = 4.74$, $p < 0.01$ [$\eta = 0.27$]; PVB and MVB reaches were found to exhibit less endpoint variability than NVB and DVB reaches ($p < 0.05$) (see Figs 3 and 4). Again, we directly compared the PVB and MVB conditions using a paired samples *t*-test. As with variable error in the primary direction, this analysis indicated that variable error in the secondary direction did not differ between the PVB and MVB conditions, $t(13) = 0.86$, $p > 0.05$ [$d = 0.48$]. As with constant error, variable error did not exhibit a visual by background condition interaction in either movement direction (primary: $F(9, 117) = 2.40$, $p > 0.05$ [$\eta = 0.17$]; secondary: $F(9, 117) = 0.53$, $p > 0.05$ [$\eta = 0.04$]).

Kinematic measures

To gauge the effects and interactions of the visual conditions, the background conditions, and the target displacement conditions, we analyzed both peak velocity and the proportion of movement time spent following peak velocity using a 4 (visual condition: OL, D0, D1000, D2000) by 4 (background condition: NVB, PVB, MVB, DVB) by 2 (target displacement: near, far) full-repeated measures ANOVA.

Analysis of peak velocity revealed main effects for visual condition, $F(3, 39) = 8.69$, $p < 0.001$ [$\eta = 0.40$], and target displacement, $F(1, 13) = 60.49$, $p < 0.001$ [$\eta = 0.82$]. Peak velocities for OL trials were greater than D0, D1000 and D2000 trials (see Fig. 2, bottom panel). The effect for target displacement indicated peak velocity increased in relation to increasing target displacement (1920 mm/s [SD 121] *versus* 2092 mm/s [SD 121]). Analysis of the proportion of movement time spent following peak velocity indicated main effects for visual condition, $F(3, 39) = 10.40$, $p < 0.001$ [$\eta = 0.44$], and target displacement, $F(1, 13) = 11.64$, $p < 0.01$ [$\eta = 0.47$]. Specifically, the proportion of movement time spent following peak velocity was less for OL (0.43 [SD 0.03]) as opposed to D0 (0.49 [SD 0.03]), D1000 (0.49 [SD 0.03]) and D2000 (0.49 [SD 0.03]) reaches ($p < 0.05$). The proportion of movement time spent following peak velocity was also found to decrease with increased target displacement (0.49 [SD 0.02] *versus* 0.46 [SD 0.02]).

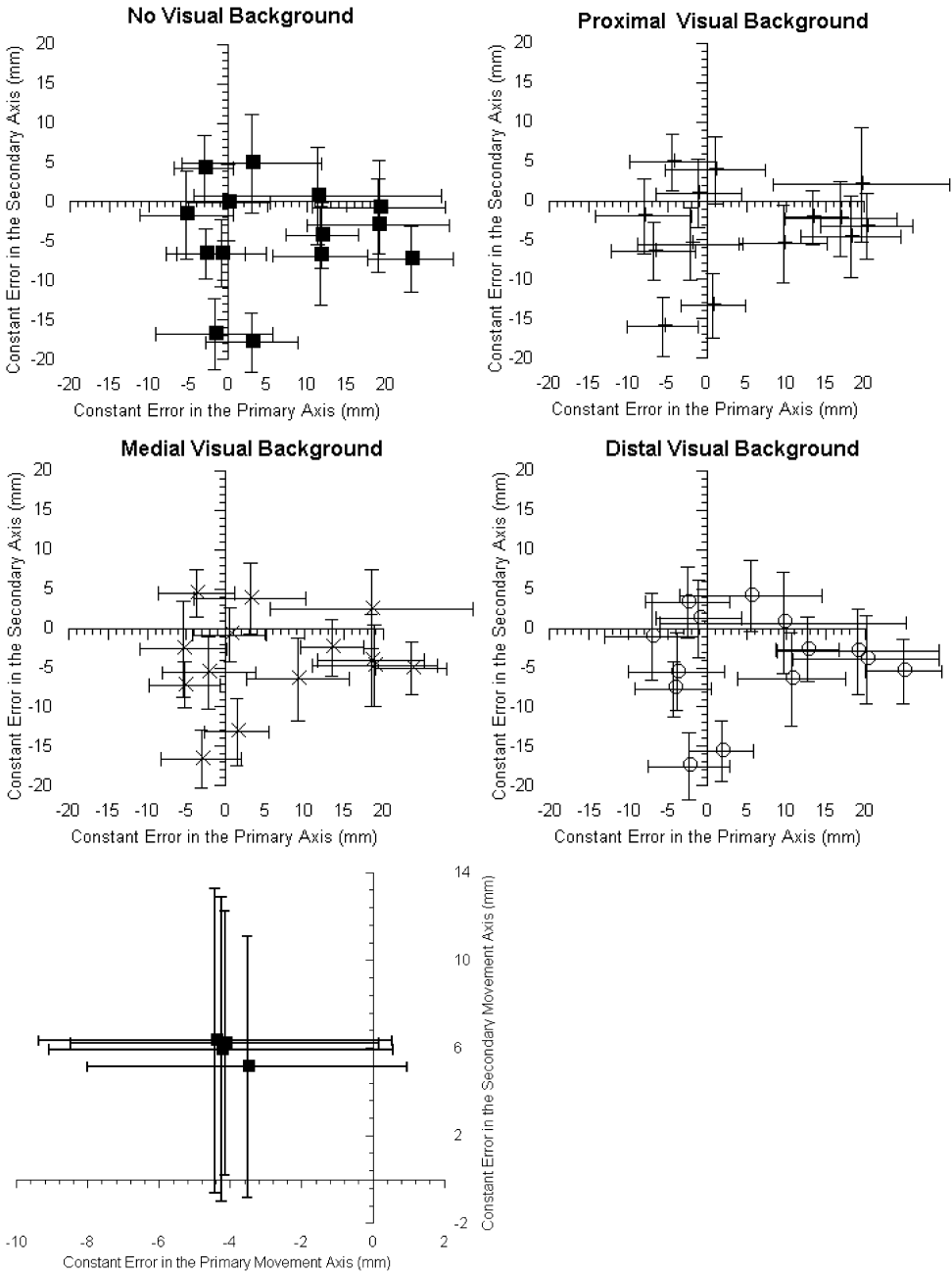


Figure 3. Top panel: Individual mean endpoint position in the primary and secondary movement axes for each background condition. Error bars represent the individual variable error values (within participant standard deviations) in each movement axis (mm). Bottom panel: Mean endpoint position (mm) in the primary and secondary movement axes as function of background condition. Error bars represent the mean variable error values (within participant standard deviations) in each movement axis (mm).

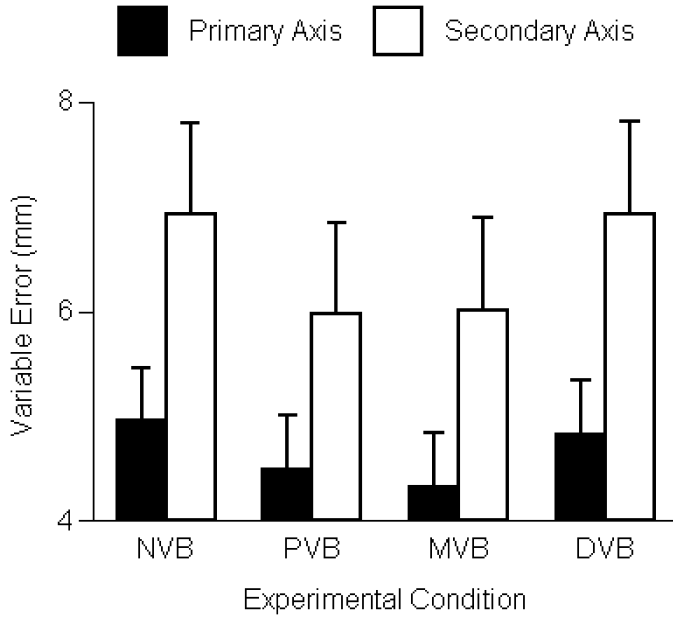


Figure 4. Variable error (mm) in the primary and secondary movement directions as a function of background condition. Error bars represent the within-participant standard deviations.

Proportion of explained endpoint variance

This analysis examined the proportion of variance (R^2) in movement endpoints explained by the position of the limb at 10% increments across the reaching trajectory. Accordingly, R^2 values in the primary movement direction were subjected to a 9 (limb position: 10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90%) by 4 (visual condition: OL, D0, D1000, D2000) by 4 (background condition: NVB, PVB, MVB, DVB) by 2 (target displacement: near, far) fully repeated-measures ANOVA. The results of this analysis indicated a main effect for limb position, $F(8, 104) = 241.26$, $p < 0.001$ [$\eta = 0.92$], and a limb position by background condition interaction, $F(24, 312) = 1.60$, $p < 0.05$ [$\eta = 0.12$]. In general we found that R^2 values increased as a function of limb position and that background conditions did not differ from 10% to 70% of reaching time ($p > 0.05$), and at 90% of the reaching trajectory. However, at 80% of the reaching trajectory we found that NVB and DVB reaches had greater R^2 values than PVB and MVB reaches ($F(3, 39) = 4.43$, $p < 0.01$ [$\eta = 0.26$]) (see Fig. 5, top panel). In order to further determine when the R^2 values differed, we also conducted separate *post-hoc* analyses of R^2 values at 75% and 85% of the reaching trajectory. Both of these analyses mirrored the results at 80%, R^2 values for PVB and MVB reaches were less than those for NVB and DVB reaches at 75% ($F(3, 39) = 2.76$, $p < 0.05$ [$\eta = 0.18$]) and at 85% ($F(3, 39) = 4.41$, $p < 0.01$ [$\eta = 0.25$]) of the reaching trajectory. Therefore, our results indicate that between 75% and 85% of the reaching trajectory PVB and MVB reaches exhibited lower R^2 values than DVB

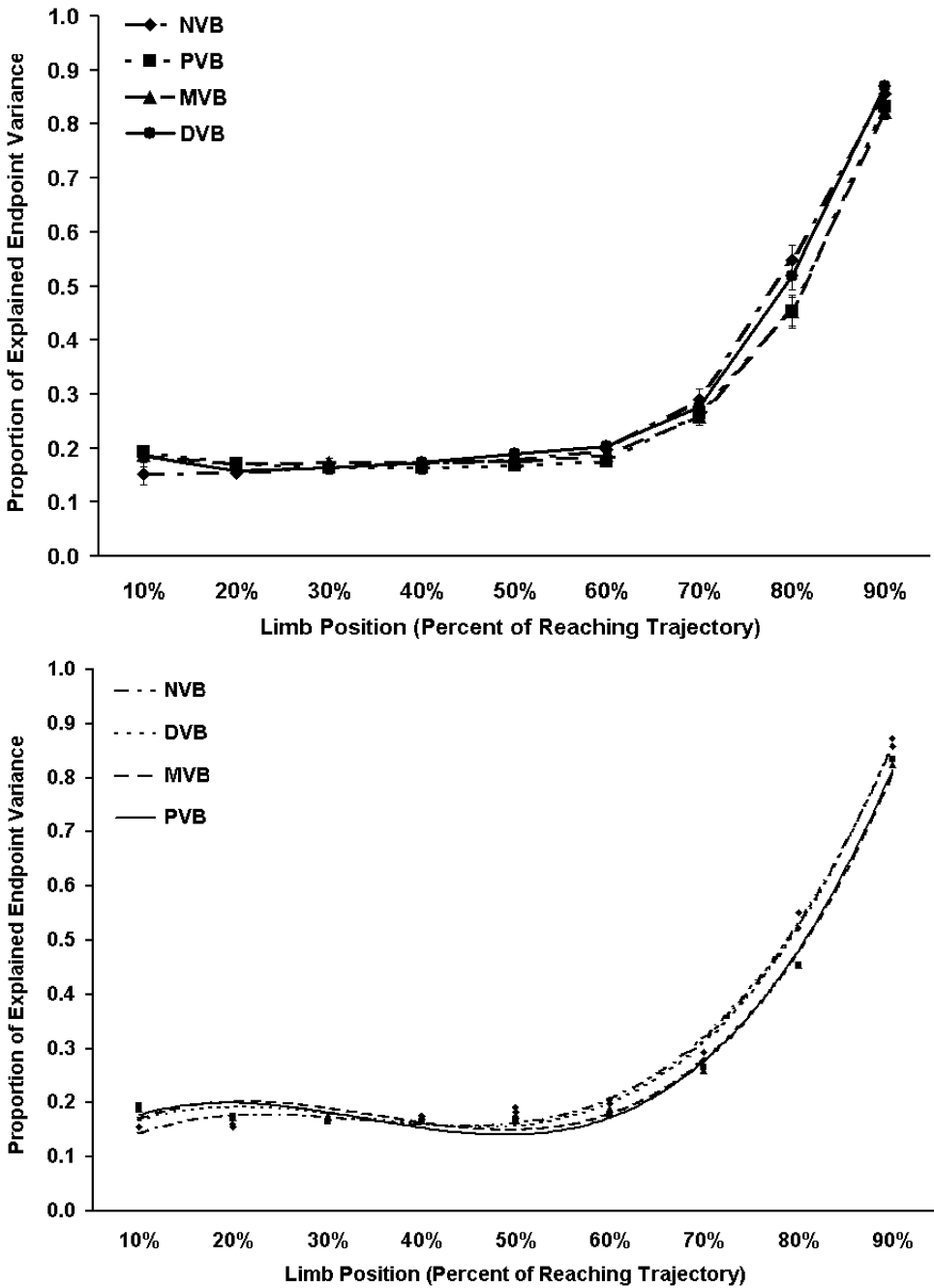


Figure 5. Top panel: Proportion of endpoint variance (R^2) explained by limb position at 10% increments of the reaching trajectory in the primary movement direction. Error bars represent the within-participant standard deviations. Bottom panel: Markers for the proportion of endpoint variance (R^2) explained by limb position at 10% increments of the reaching trajectory in the primary movement direction fitted with third-order polynomials.

Table 1.

Equations for the third-order polynomials fit to the incremental trajectory markers for the NVB, PVB, MVB and DVB conditions

NVB:	$y = 0.0044x^3 - 0.0446x^2 + 0.1365x + 0.0449$
PVB:	$y = 0.0047x^3 - 0.0479x^2 + 0.1334x + 0.0854$
MVB:	$y = 0.0048x^3 - 0.0506x^2 + 0.1503x + 0.0639$
DVB:	$y = 0.0045x^3 - 0.0448x^2 + 0.1277x + 0.0782$

and NVB reaches. Finally, the conducted trend analyses on the R^2 values across the reaching trajectory for each background condition. These analyses indicated that for each background condition a third-order polynomial could be fit to the data (NVB: $F(1, 13) = 67.32$, $p < 0.001$; PVB: $F(1, 13) = 68.03$, $p < 0.001$; MVB: $F(1, 13) = 147.70$, $p < 0.001$; DVB: $F(1, 13) = 68.92$, $p < 0.001$) (see Fig. 5, bottom panel; also see Table 1 for the third-order polynomial equations). Visual inspection of these polynomials indicated a divergence between the NVB, DVB and the PVB, MVB conditions between 50% to 60% of the reaching trajectory.

DISCUSSION

A series of recent studies have demonstrated that framing a target within a visual background enhances the accuracy and consistency of memory-guided reaches (Barry *et al.*, 1997; Carrozzo *et al.*, 2002; Krigolson and Heath, 2004; Lemay *et al.*, 2004; Obhi and Goodale, 2005; Sheth and Shimojo, 2004). The goal of the present research was to determine whether the proximity between a target and visual landmarks influences the effectiveness by which allocentric cues can be used to enhance reaching performance.

The impact of increasing memory delays

In spite of Elliott and Madelana's (1987) assertion that a highly accurate representation of the reaching environment is available for delay periods of up to two seconds, a growing body of evidence suggests that memory representations begin to degrade immediately following visual occlusion (Binsted *et al.*, 2006; Heath and Westwood, 2003; Heath *et al.*, 2004a; Westwood *et al.*, 2000, 2001, 2003). As such, increased visual delays of target information in advance of a reaching movement typically results in an increase in endpoint error and/or variability (see Heath, 2005). The results of the present study are consistent with this prediction as we found that constant error in the primary movement direction increased between the open-loop and memory-guided conditions. Our results for movement time and peak velocity demonstrated that OL reaches had shorter movement times and larger peak velocities than D0, D1000 and D2000 reaches. Importantly, these data rule out the possibility of a speed-accuracy trade-off (*cf.* Fitts, 1954) explanation for the observed increase in endpoint error. Instead, our results support the hypothesis that

memory-guided reaches are less accurate and more variable than open-loop reaches due to a decay of the movement representation used to plan and control the reaching movement (Westwood *et al.*, 2001, 2003). Note that the trend in endpoint error was not apparent in the secondary movement direction, a result in line with other studies which have not found increased directional error with increasing memory delays (Krigolson and Heath, 2004).

The effect of visual background proximity

In the present study the availability of a visual background resulted in reduced endpoint variability in the PVB and MVB conditions relative to the NVB condition. Importantly, this result suggests that participants were able to make comparisons between the proximal and medial visual backgrounds to stabilise the remembered target location (*cf.* Krigolson and Heath, 2004). Interestingly, however, we found that endpoint variability was not reduced in the DVB relative to the NVB condition. Taken together, these results indicate that although allocentric comparisons between a remembered target and a visual background can reduce endpoint variability, the effectiveness of these comparisons is reduced with increased displacement between the visual background and the remembered target. In line with our results, Keller *et al.* (2005) demonstrated that the effectiveness of allocentric visual comparisons is reduced with displacement using a line bisection task. Specifically, Keller *et al.* found that participants were more accurate when making proximal as opposed to distal line bisections; a task thought to rely on allocentric visual comparisons. From their results, Keller and colleagues concluded that displacement changes perception within an allocentric reference frame and, as such, actions performed within this frame would suffer reduced accuracy with increasing displacement. It is worth noting that the results of the present study indicated that the availability of a visual background did not improve accuracy, a result contrary to a previous finding (Krigolson and Heath, 2004). One possible reason the visual background did not facilitate reaching accuracy in the present study may stem from the small number of trials employed in each experimental condition. Indeed, the natural variability associated with a small number of trials may have masked visual background effects on movement accuracy.

In spite of this, the reduction in endpoint variability in the PVB and MVB conditions suggests that the availability of a visual background helped to stabilise a remembered target location. Interestingly, allocentric visual background-remembered target comparisons reduced endpoint variability in MVB as compared to DVB, but not when comparing PVB to MVB. More research is needed to specifically ascertain why this relationship is non-linear; at this point we can only speculate that this relationship is similar to other non-linear decay patterns (*i.e.* the memory representation used to guide reaches to a remembered target appears to decay in a non-linear fashion: Binsted *et al.*, 2006; Keele, 1968; Woodworth, 1899).

How does the availability of a visual background improve reaching consistency? When a reaching movement is made to a remembered target not framed within a vi-

sual background, movement planning and online control mechanisms are primarily dependent upon egocentric comparisons between the remembered target location and the movement effector (Beggs and Howarth, 1972; Carlton, 1979, 1981; Crossman and Goodeve, 1983; Keele, 1981; McIntyre *et al.*, 1997, 1998). However, when a visual background is available it is also possible to make allocentric comparisons between the remembered target location and the background landmarks to improve the estimate of the remembered target location (*cf.* Krigolson and Heath, 2004; Obhi and Goodale, 2005). Together, previous research (e.g. Krigolson and Heath, 2004) combined with the results of the present study suggest that egocentric and allocentric visual information can be integrated to reduce endpoint variability.

Seminal work by Goodale and Milner (1992) proposed that there were separate visual pathways for action and perception — the dorsal and ventral visual streams. Typically, the processing of egocentric visual information is associated with the dorsal stream whereas the processing of allocentric visual information is associated with the ventral stream. As such, the results of the present study are counter to a strict interpretation of the action-perception model. However, recent research examining the action-perception model suggests that interactions occur between the two visual streams (*cf.* Goodale and Westwood, 2004). Indeed, a growing body of evidence examining the impact of visual backgrounds (Conti and Beaubaton, 1980; Krigolson and Heath, 2004; Obhi and Goodale, 2005; Toni *et al.*, 1996; Velay and Beaubaton, 1986) and visual illusions (Carrozzo *et al.*, 2002; Gentilucci *et al.*, 1996; Gentilucci and Negrotti, 1994; Heath *et al.*, 2004b; Heath *et al.*, 2006; Hu and Goodale, 2000) strongly suggests that information from both the dorsal and ventral visual streams can be integrated to facilitate reaching accuracy and/or consistency.

What mechanism underlies allocentric visual background-remembered target comparisons? One potential explanation is that the availability of a visual background provides visual motion cues that allow a participant to make online amendments to reaching movements in response to ego-motion. In other words, a visual background may provide a visual motion cues that allow the participants to update a reaching trajectory in response to head and/or eye movements. In a series of experiments Whitney *et al.* (2003) found that movement endpoints of rapid reaching movements were biased in parallel to the motion of a distant moving background. Interestingly, this result suggests that motion signals derived from head and eye movements can be utilised to update a target location. As such, the results of the present study suggest that a visual background sufficiently close to a remembered target location can be used as a visual motion cue to correct for movement error brought about by ego-motion.

An alternative mechanism that explains the results of the present study relates to the spatial frequency provided by the visual background. Specifically, if one considers the visual background in terms of spatial frequency (i.e. the PVB has a higher spatial frequency than the DVB), it seems plausible that that higher spatial frequencies would afford more precise landmarks for comparison purposes. As such, aiming movements to a target framed within a high spatial frequency

background would be less variable than reaches made to targets presented within a low spatial frequency background, a proposal consistent with the results of the present study.

Our results suggest that the allocentric visual background — remembered target comparisons primarily influenced the effectiveness of online, feedback-based control processes. Specifically, our analysis of the proportion of endpoint variance explained by limb position indicated that from 75% to 85% of the reaching trajectory PVB and MVB reaches had lower R^2 values than DVB and NVB reaches (see Fig. 4). Recall that in this type of analysis lower R^2 values are associated with increased online control (for more detail on the theoretical reasoning behind this analysis technique see Heath *et al.*, 2004a; see also Heath, 2005). Thus, the results of the present study suggest that from somewhere between 70% and 75% to 85% of the reaching trajectory participants were engaged in greater online movement corrections in the PVB and NVB relative to the DVB and NVB conditions. Notably, this result parallels earlier work showing that R^2 values were lower at peak deceleration on trials when a visual background was available (Krigolson and Heath, 2004). Furthermore, the reduced R^2 phase of the reaching trajectory (75%) occurred significantly after peak velocity (which occurred on average at 55% of the reaching trajectory), a timeframe consistent with previous accounts of when online control occurs during goal directed reaching movements (Chua and Elliott, 1993; Elliott *et al.*, 1991).

Although the results of the present study suggest that the availability of a visual background facilitates online control processes, one cannot rule out the possibility that the availability of a visual background assists movement planning. For example, Obhi and Goodale (2005) recently reported that allocentric visual information can be used to facilitate movement planning processes. In their experiment, Obhi and Goodale had participants perform memory-guided reaching movements to targets framed within a visual background that was removed coincident with movement onset. Obhi and Goodale's results indicated that accuracy was enhanced by the availability of a visual background during movement planning, a result suggesting that allocentric visual comparisons may assist in estimating target location. However, as mentioned previously, our results (i.e. the regression analysis employed in the present experiment) strongly suggest that allocentric comparisons facilitate the online control of memory-guided reaching movements. Indeed, we did not find conditional differences (PVB, MVB *versus* DVB, NVB) in the R^2 analysis at earlier points in the reaching trajectory (i.e. 25% and/or 50%) indicating that in the present experiment the visual background did not facilitate movement planning. Instead, we only found differences between the background conditions late in the reaching trajectory (75%), a result suggesting that the availability of a visual background facilitated online control processes (Binsted and Heath, 2004; Elliott *et al.*, 1999; Heath, 2005; Heath *et al.*, 2004b; Krigolson and Heath, 2004). One possible reconciliation of these findings is that allocentric visual comparisons may be taken advantage of whenever possible. In other words, if allocentric comparisons are only

possible at movement planning then this is when the information is utilised. Conversely, if allocentric comparisons can be made during a reaching movement then the motor system will take advantage of this information to enhance online control processes.

CONCLUSIONS

The results of the present study suggest allocentric comparisons between a remembered target and a visual background can be used to stabilise target location and reduce endpoint variability via the evocation of limb adjustments late in the reaching trajectory. Further, the present results show that increased displacement between structured visual context and veridical target location diminishes the extent allocentric cues are used to guide reaching performance. Finally, the results of the present study combined with other research (i.e. Obhi and Goodale, 2005) suggest that both egocentric and allocentric visual information can be utilised to facilitate reaching accuracy/consistency, a finding counter to a strict interpretation of the action-perception model.

NOTES

1. In previous work (i.e. Krigolson and Heath, 2006) where we did use eye tracking equipment we found that participants strictly adhered to the instruction to maintain their eyes on the target location. As such, we did not feel that it was necessary to record eye movements in the present experiment.
2. It is worth noting that the filtering process may have biased our estimate of movement onset, resulting in longer or shorter movement times than what are reported here. However, we feel that these differences would be similar across all experimental conditions.

REFERENCES

- Barry, S. R., Bloomberg, J. J. and Huebner, W. P. (1997). The effect of visual context on manual localization of remembered targets, *NeuroReport* **8**, 468–473.
- Beggs, W. D. and Howarth, C. I. (1972). The accuracy of aiming at a target: some further evidence for a theory of intermittent control, *Acta Psychologica* **30**, 171–177.
- Binsted, G. and Heath, M. (2004). Can the motor system utilize a stored representation to control movement? *Behavioral and Brain Sciences* **27**, 25–27.
- Binsted, G. and Heath, M. (2005). No evidence of a lower visual field specialization for visuomotor control, *Exper. Brain Res.* **162**, 89–94.
- Binsted, G., Rolheiser, T. and Chua, R. (2006). Decay in visuomotor representations during manual aiming, *J. Motor Behavior* **38**, 82–87.
- Carlton, L. G. (1979). Control processes in the production of discrete aiming responses, *J. Human Movement Studies* **5**, 115–124.

- Carlton, L. G. (1981). Visual information: the control of aiming movements, *Quart. J. Exper. Psychol.* **33A**, 87–93.
- Carozzo, M., Stratta, F., McIntyre, J. and Lacquaniti, F. (2002). Cognitive allocentric representations of visual space shape pointing errors, *Exper. Brain Res.* **147**, 426–436.
- Chua, R. and Elliott, D. (1993). Visual regulation of manual aiming, *Human Movement Science* **12**, 365–401.
- Coello, Y. and Greally, M. A. (1997). Effect of size and frame of visual field on the accuracy of an aiming movement, *Perception* **26**, 287–300.
- Conti, P. and Beaubaton, D. (1980). Role of structured visual field and visual reafference in accuracy of pointing movements, *Perceptual and Motor Skills* **50**, 239–244.
- Crossman, E. R. and Goodeve, P. J. (1983). Feedback control of hand-movement and Fitts Law, *Quart. J. Exper. Psychol.: Human Exper. Psychol.* **35A**, 251–278.
- Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E. and Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target, *Nature Neuroscience* **2**, 563–567.
- Desmurget, M., Grea, H., Grethe, J. S., Prablanc, C., Alexander, G. E. and Grafton, S. T. (2001). Functional anatomy of nonvisual feedback loops during reaching: a positron emission tomography study, *J. Neurosci.* **21**, 2919–2928.
- Elliott, D. (1988). The influence of visual target and limb information on manual aiming, *Canad. J. Psychol.* **42**, 57–68.
- Elliott, D. and Madalena, J. (1987). The influence of premovement visual information on manual aiming, *Quart. J. Exper. Psychol.* **39A**, 541–559.
- Elliott, D., Carson, R. G., Goodman, D. and Chua, R. (1991). Discrete vs. continuous visual control of manual aiming, *Human Movement Science* **10**, 393–418.
- Elliott, D., Heath, M., Binsted, G., Ricker, K. L., Roy, E. A. and Chua, R. (1999). Goal-directed aiming: correcting a force specification error with the right and left hands, *J. Motor Behavior* **31**, 309–324.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement, *J. Exper. Psychol.* **48**, 303–312.
- Gentilucci, M. and Negrotti, A. (1994). Dissociation between perception and visuomotor transformation during reproduction of remembered distances, *J. Neurophysiol.* **72**, 2026–2030.
- Gentilucci, M., Chieffi, S., Deprati, E., Saetti, M. C. and Toni, I. (1996). Visual illusion and action, *Neuropsychologia* **34**, 369–376.
- Goodale, M. A. (2005). Action insight: the role of the dorsal stream in the perception of grasping, *Neuron* **47**, 328–329.
- Goodale, M. A. and Humphrey, G. K. (1998). The objects of action and perception, *Cognition* **67**, 181–207.
- Goodale, M. A. and Milner, A. D. (1992). Separate visual pathways for perception and action, *Trends in Neuroscience* **15**, 20–25.
- Goodale, M. A. and Westwood, D. A. (2004). An evolving view of duplex vision: separate but interacting cortical pathways for perception and action, *Current Opinion in Neurobiology* **14**, 203–211.
- Goodale, M. A., Westwood, D. A. and Milner, A. D. (2004). Two distinct modes of control for object-directed action, *Prog. Brain Res.* **144**, 131–144.
- Grandt, J. W. and Andersen, R. A. (1987). Memory related motor planning activity in posterior parietal cortex of macaque, *Exper. Brain Res.* **70**, 216–220.
- Grea, H., Pisella, L., Rossetti, Y., Desmurget, M., Tilikete, C., Grafton, S., Prablanc, C. and Vighetto, A. (2002). A lesion of posterior parietal cortex disrupts on-line adjustments during aiming movements, *Neuropsychologia* **40**, 2471–2480.
- Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches, *Motor Control* **9**, 281–311.

- Heath, M. and Westwood, D. A. (2003). Does a visual representation support the online control of memory-dependent reaching? Evidence from a variable spatial mapping paradigm, *Motor Control* **7**, 346–361.
- Heath, M., Westwood, D. A. and Binsted, G. (2004a). The control of memory-guided reaching movements in peripersonal space, *Motor Control* **8**, 76–106.
- Heath, M., Rival, C. and Binsted, G. (2004b). Can the motor system resolve a premovement bias in grip aperture? Online analysis of grasping the Muller–Lyer illusion, *Exper. Brain Res.* **158**, 378–384.
- Heath, M., Rival, C., Westwood, D. A. and Neely, K. (2005). Time course analysis of closed- and open-loop grasping of the Muller–Lyer illusion, *J. Motor Behavior* **37**, 179–185.
- Heath, M., Rival, C., Neely, K. and Krigolson, O. (2006). Muller–Lyer figures influence the online reorganization of visually guided grasping movements, *Exper. Brain Res.* **169**, 473–481.
- Hu, Y. and Goodale, M. A. (2000). Grasping after a delay shifts size-scaling from absolute to relative metrics, *J. Cognit. Neurosci.* **12**, 856–868.
- Keele, S. W. (1968). Movement control in skilled motor performance, *Psychol. Bull.* **70**, 387–403.
- Keele, S. W. (1981). Behavioral analysis of movement. In: V. Brooks (Ed.), *Handbook of physiology: Section 1: The nervous system, Vol. II. Motor control, Part 2* (pp. 1391–1414). American Physiological Society, Baltimore, MD.
- Keller, I., Schindler, I., Kerkhoff, G., von Rosen, F. and Golz, D. (2005). Visuospatial neglect in near and far space: dissociation between line bisection and letter cancellation, *Neuropsychologia* **43**, 724–731.
- Khan, M. A., Elliott, D., Coull, J., Chua, R. and Lyons, J. (2002). Optimal control strategies under different feedback schedules: kinematic evidence, *J. Motor Behavior* **34**, 45–58.
- Krigolson, O. E. and Heath, M. (2004). Background visual cues and memory-guided reaching, *Human Movement Science* **23**, 861–877.
- Krigolson, O. E. and Heath, M. (2006). A lower visual field advantage for endpoint stability but no advantage for online movement precision, *Exper. Brain Res.* **170**, 127–135.
- Lemay, M., Bertram, C. P. and Stelmach, G. E. (2004). Pointing to an allocentric and egocentric remembered target, *Motor Control* **8**, 16–32.
- Loftus, G. R. and Masson, M. E. J. (1994). Using confidence intervals in within-subject designs, *Psychonomic Bull. Rev.* **1**, 476–490.
- McIntyre, J., Stratta, F. and Lacquaniti, F. (1997). A viewer centered reference frame for pointing to memorized targets in three-dimensional space, *J. Neurophysiol.* **78**, 1601–1618.
- McIntyre, J., Stratta, F. and Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: psychophysical evidence for body-centered reference frames, *J. Neurosci.* **18**, 8423–8435.
- Masson, M. E. J. and Loftus, G. R. (2003). Using confidence intervals for graphically based data interpretation, *Canad. J. Exper. Psychol.* **57**, 203–220.
- Milner, A. D. and Goodale, M. A. (1995). *The Visual Brain in Action*. Oxford University Press, Oxford, UK.
- Obhi, S. S. and Goodale, M. A. (2005). The effects of landmarks on the performance of delayed and real-time pointing movements, *Exper. Brain Res.* **167**, 335–344.
- Pisella, L., Grea, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., Boisson, D. and Rossetti, Y. (2000). An ‘automatic pilot’ for the hand in human posterior parietal cortex: toward reinterpreting optic ataxia, *Nature Neuroscience* **3**, 729–736.
- Proteau, L. and Masson, G. (1997). Visual perception modifies goal-directed movement control: supporting evidence from a visual perturbation paradigm, *Qtrly J. Exper. Psychol.* **50**, 726–741.
- Sheth, B. R. and Shimojo, S. (2004). Extrinsic cues suppress the encoding of intrinsic cues, *J. Cognit. Neurosci.* **16**, 339–350.
- Toni, I., Gentilucci, M., Jeannerod, M. and Decety, J. (1996). Differential influence of the visual framework on end point accuracy and trajectory specification of arm movements, *Exper. Brain Res.* **111**, 447–454.

- Velay, J. L. and Beaubaton, D. (1986). Influence of visual context on pointing movement accuracy, *Cahiers de Psychologie Cognitive* **6**, 447–456.
- Westwood, D. A. and Goodale, M. A. (2003). Perceptual illusion and the real-time control of action, *Spatial Vision* **16**, 243–254.
- Westwood, D. A., Heath, M. and Roy, R. A. (2000). The effect of pictorial illusion on closed-loop and open-loop prehension, *Exper. Brain Res.* **134**, 456–463.
- Westwood, D. A., Heath, M. and Roy, E. A. (2001). The accuracy of reaching movements in brief delay conditions, *Canad. J. Exper. Psychol.* **55**, 304–310.
- Westwood, D. A., Heath, M. and Roy, E. A. (2003). No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching, *J. Motor Behavior* **35**, 127–134.
- Whitney, D., Westwood, D. A. and Goodale, M. A. (2003). The influence of visual motion on fast reaching movements to a stationary target, *Nature* **423**, 869–873.
- Winter, D. A. and Patla, A. E. (1997). *Signal Processing and Linear Systems for Movement Sciences*. Waterloo Biomechanics, Waterloo, Ontario, Canada.
- Woodworth, R. S. (1899). The accuracy of voluntary movement, *Psychol. Rev.* **3**, 1–114.

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