

Response Modes Influence the Accuracy of Monocular and Binocular Reaching Movements

Matthew Heath, Kristina Neely, and Olav Krigolson

The authors manipulated the availability of monocular and binocular vision during the constituent planning and control stages of a goal-directed reaching task. Furthermore, trials were completed with or without online limb vision to determine whether monocular- or binocular-derived ego-motion cues influence the integration of visual feedback for online limb corrections. Results showed that the manipulation of visual cues during movement planning did not influence planning times or overall kinematics. During movement execution, however, binocular reaches—and particularly those completed with online limb vision—demonstrated heightened endpoint accuracy and stability, a finding directly linked to the adoption of a feedback-based mode of reaching control (i.e., online control). In contrast, reaches performed with online monocular vision produced increased endpoint error and instability and demonstrated reduced evidence of feedback-based corrections (i.e., offline control). Based on these results, the authors propose that the combination of static (i.e., target location) and dynamic (i.e., the moving limb) binocular cues serve to specifically optimize online reaching control. Moreover, results provide new evidence that differences in the kinematic and endpoint parameters of binocular and monocular reaches reflect differences in the extent to which the aforementioned engage in online and offline modes of movement control.

Keywords: binocular cues, kinematics, feedback, monocular cues, reaching

Retinal disparities, angle of convergence, and ego-motion cues arising from binocular vision are thought to provide the visuomotor system absolute object and egocentric limb information optimizing the efficiency and effectiveness of goal-directed actions (Previc, 1998). One logical assumption concerning binocular vision is that it provides a unitary benefit facilitating the distinct visuomotor channels thought to underlie the limb transport and aperture-shaping components of prehension (for review see Jeannerod, 1986), as well as optimizing the independent planning and control mechanisms subserving prehension and simple reaching responses (e.g., Woodworth, 1899; for review see Elliott, Helsen, & Chua, 2001). There is, however, debate in the visuomotor neurosciences regarding the perva-

Heath and Neely are with the School of Kinesiology, University of Western Ontario, London, Ontario, Canada N6A 3K7. Krigolson is with the Dept. of Psychology, University of Victoria, Victoria, British Columbia, Canada V8W 3P5.

siveness by which binocular signals globally influence the constituent elements of goal-directed action.

Several experiments beginning with Servos and Goodale (e.g., Servos, Goodale, & Jakobson, 1992; Servos & Goodale, 1994; Servos, 2000) have demonstrated that binocular vision concurrently benefits limb transport and aperture shaping. Specifically, Servos et al. reported that the transport phase of monocular grasping movements elicits reduced peak velocities and increased deceleration times relative to binocular ones, and monocular grasps were shown to produce smaller peak grip apertures than binocular counterparts (see also Servos, 2000).¹ According to the authors, such a pattern of results indicates that binocular, but not monocular, vision provides metrical sensorimotor transformations necessary for the specification of both egocentric target distance and absolute target size. It is, however, important to note that Bradshaw and colleagues reported a dissociative influence of binocular vision on limb transport and aperture shaping (e.g., Bradshaw et al., 2004; Watt & Bradshaw, 2000; see also Marotta, Behrmann, & Goodale, 1997). In one study involving closed-loop grasps (i.e., vision continuously available to the performer), Watt and Bradshaw (2000) reported no difference in limb transport kinematics across binocular and monocular actions; rather, results showed a restrictive influence on aperture formation such that monocular grasps yielded larger peak grip apertures than binocular ones (cf. Bradshaw & Elliott, 2003). In a second study involving open-loop grasps (i.e., vision occluded at movement onset), Bradshaw et al. (2004) reported the opposite effect; that is, the removal of binocular vision influenced the scaling of limb transport but not the specification of grip aperture. Bradshaw and colleagues provided an interesting set of findings inasmuch as they suggest that binocular vision can independently influence the component elements of prehension. More specifically, their results indicate that in the absence of online limb vision, binocular signals available at the time of response planning play an important role in specifying egocentric target distance (i.e., specifying limb transport kinematics). In contrast, binocular cues related to target size are reportedly more heavily weighted under conditions wherein continuous visual contact with a target object permits visually based comparisons (e.g., Heath, Westwood, & Binsted, 2004) between unfolding grip aperture and the to-be-grasped target.

That binocular vision differentially influences the constituent elements of prehension dependent on the presence or absence of online visual feedback suggests that the putative planning and control mechanisms of goal-directed action might also be independently influenced by stereoscopic cues (for reviews see Elliott et al., 2001, or Glover, 2004). Once again Servos and Goodale (1994) provide the first direct examination of this issue via separate experiments wherein binocular cues were manipulated during the response planning (i.e., Experiment 2) and the response execution (i.e., Experiment 1) phases of prehension. The authors reported that grasps performed with online monocular as opposed to online binocular vision yielded prolonged movement durations linked to an increase in limb deceleration (compare Experiment 1 and 2). Moreover, the aperture profiles of grasps associated with an initial monocular view (i.e., at the time of response planning) showed an increase in the time required to achieve a stable contact with target objects. Based on the above results, Servos and Goodale concluded that binocular vision enhances movement planning by providing “better” information concerning the size and location of an object and by optimizing visually based effector/target corrections

(see also Loftus, Servos, Goodale, Mendarozqueta, & Mon-Williams, 2004). In other words, and in line with their original work (e.g., Servos et al., 1992), results suggest that binocular cues provide a unitary advantage benefiting constituent visuomotor processes.

Similar to the extant results for limb transport and aperture shaping, the manner and degree to which binocular vision facilitates movement planning and control is not without controversy. One such controversy surrounds Servos and Goodale's (1994) assertion that binocular vision advantages movement planning. Indeed, Melmoth and Grant (2006) reported that closed-loop grasping movements initiated with "a monocular view contains sufficient distance information to adequately programme the early phase of hand transport" (p. 383). In addition, Coull and colleagues (Coull, Weir, Tremblay, Weeks, & Elliott, 2000) report no difference in the overall timing, accuracy, and endpoint variability of open-loop reaching movements implemented on the basis of monocular or binocular vision. Thus, more recent results suggest movement planning processes are not dependent on absolute visual information; rather, results are in line with the view that the early kinematic parameterization of action entails only the relative, as opposed to the absolute, goal of bringing the effector into the vicinity of the target (Glover, 2004).

A second controversy surrounds the manner in which binocular vision facilitates the online control of action. From the extant literature it is clear that closed-loop responses performed with monocular vision are completed more slowly and exhibit a specific increase in movement deceleration relative to binocular counterparts (e.g., Bradshaw & Elliott, 2003; Bradshaw et al., 2004; Loftus et al., 2004; Melmoth & Grant, 2006; Servos et al., 1992; Servos & Goodale, 1994; Westwood, Robertson, & Heath, 2005; but see Experiment 4 of Coull et al., 2000). That finding is frequently held as evidence of a reduced ability to use monocular cues to implement quick and accurate feedback-based corrections for online trajectory modifications. It is, however, likely that a reduction in the quality of online visual information associated with monocular input necessitates that the performer adopt a mode of control quite different from binocular responses. Indeed, our group has shown that when vision of the movement environment is degraded by reducing the availability of online limb vision (Heath, Rival, & Binsted, 2004; Heath & Binsted, 2007) or by diminishing the validity of cue-defined target information (Heath & Westwood, 2003; Krigolson & Heath, 2004; Krigolson, Clark, Heath, & Binsted, 2007), then reaches are specified primarily in advance of movement onset via central planning mechanisms (Heath, 2005). In this offline mode of control, overall movement duration—and the deceleration phase of the trajectory—can be increased without concomitant discrete and/or continuous feedback-based corrections to the movement trajectory. It is therefore entirely possible that the prolonged deceleration phase of monocular reaches reflects the instantiation of an offline mode of control to account for visuomotor uncertainty.

In the current investigation, we manipulated the availability of monocular and binocular vision at movement planning and control with a condition wherein limb vision was available or unavailable during goal-directed reaching movements. The aforementioned experimental conditions were used to address three outstanding issues related to monocular and binocular movement control. First, participants planned their responses using monocular or binocular vision, and the same (e.g., monocular planning and monocular control) or altered (e.g., monocular planning

and binocular control) visual condition was provided during movement execution. This factorial combination provides the first direct (i.e., within-experiment) examination of the independent or conjoint impact of viewing conditions on movement planning and control. Indeed, if binocular vision asserts a unitary performance advantage on goal-directed action, then both early and late kinematics of binocular responses should demonstrate distinct performance advantages (i.e., faster and less variable) over monocular counterparts. Second, we examined whether the heightened deceleration phase reported for monocular actions underlies differences in the efficiency by which visual feedback is used for online limb corrections or the adoption of a distinct mode of movement control (i.e., online versus offline). By limiting our response to a simple reaching, as opposed to grasping, paradigm, we are able to infer movement control by examining limb trajectory parameters without the contemporaneous influence of grip aperture formation (see Heath, Westwood, et al., 2004). Third, we sought to determine whether binocular cues are weighted more heavily under conditions wherein continuous limb vision can be compared with veridical target location. Indeed, if ego-motion signals enhance the weighting of binocular vision for movement control via integration of stereomotion and diplopic images of the moving limb, than binocular responses performed with limb vision should produce limb trajectories that are controlled more online relative to a situation wherein only a binocular view of the target is provided (i.e., the limb is occluded) or a situation wherein strict monocular input is available.

Methods

Participants

Twelve participants (6 men, 6 women; age range = 21–28 years) were recruited from the Indiana University student population. Participants were right-handed as determined by a modified version of the University of Waterloo Handedness Questionnaire (Bryden, 1977), had normal or corrected-to-normal vision (contact lenses only), and demonstrated right eye dominance as determined by a version of the “hole in hand test” (Miles, 1930). Participants gave informed consent and the Human Subjects Committee, Indiana University, approved this study.

Apparatus and Procedure

We used an aiming apparatus similar to that introduced by Held and Gottlieb (1958; see Krigolson & Heath, 2006, for complete details). The apparatus was placed on a normal tabletop and consisted of a two-sided box containing an upper shelf that supported a computer monitor (NEC Multisync model 1765; 16-ms response rate), a one-way mirror (which divided the apparatus in half), and a lower/reaching surface. The computer monitor was used to project visual stimuli on the mirror surface, and the optical geometry of the setup allowed that visual stimuli projected on the mirror appeared to participants as being on the lower/reaching surface of the apparatus. A constant optical geometry was maintained via a head-chin rest (Lafayette Instruments, model 14302, Lafayette, IN).

Participants sat at an open end of the apparatus, and from a midline home position (a microswitch) completed goal-directed reaches using their right index

finger to midline targets located in the depth plane. Targets were 1-cm diameter red circles presented against a high-contrast black background located 30 (i.e., the near target) and 35 (i.e., the far target) cm from the home position. Direct viewing of the reaching limb (i.e., underneath the one-way mirror) was prevented by darkening the experimental suite, and in the place of veridical limb vision, two light-emitting diodes (LEDs) affixed to a splint complex and attached to the nail of the reaching finger (i.e., the right index finger) were used to provide visual feedback about limb position. Liquid-crystal shutter goggles (PLATO Technologies, Toronto, ON, Canada) controlled monocular and binocular visual input. By making the right, but not left, lens of the liquid-crystal goggles transparent (i.e., the left lens was set in its normally translucent or “closed” state), participants were provided monocular visual input. Of course, allowing for transparency of both right and left lenses allowed for binocular visual input. Visual and auditory events were controlled via Eprime (ver 1.1: Psychology Software Tools, Pittsburgh, PA, USA).

An individual trial began when participants placed their index finger on the home position. That action resulted in the projection of the near or the far target for a 1,500-ms preview period after which point an auditory tone cued participants to implement a “fast and accurate” reaching movement (the target remained continuously visible). Trials were performed in four conditions involving the factorial combination of monocular and binocular vision at response planning (i.e., the time from initial target viewing to movement onset) and control (i.e., the time from movement onset to movement offset), as well as two conditions involving the manipulation of limb vision (limb-visible versus limb-occluded trials). For the manipulation of monocular and binocular vision, one trial block involved monocular vision during response planning and control (MM), a second trial block involved monocular vision during response planning and binocular vision during response control (MB), a third trial block involved binocular vision during response planning and control (BB), and a fourth block involved binocular vision during response planning and monocular vision during response control (BM). For the trial blocks involving a within-trial transition of stereopsis (i.e., the MB and BM trial blocks), the transition occurred at movement onset (i.e., release of pressure from the home position). In terms of the manipulation of limb vision, the LEDs representing the limb were illuminated at the start of each trial (i.e., when the home position was pressed). For limb-visible trials, the LEDs remained illuminated throughout a response, whereas the LEDs were extinguished at movement onset for limb-occluded trials.

The factorial arrangement of monocular and binocular vision (as discussed earlier) produced four separate and randomly ordered blocks of trials (i.e., MM, MB, BB, BM). Within each trial block, limb-visible and limb-occluded trials were organized separately (via randomly ordered blocks), and 20 limb-visible and 20 limb-occluded trials were completed to each of the near and far targets (organized pseudo-randomly) for a total of 320 experimental trials.

Data Collection and Reduction

In addition to containing dual LEDs, the splint complex attached to the pointing finger contained an infrared emitting diode (IRED). IRED position data were sampled at 200 Hz for 1 s following the auditory initiation tone via an OPTOTRAK 3020 (Northern Digital Inc., Waterloo, ON, Canada). Offline, displacement data

were filtered via a second-order, dual-pass Butterworth filter employing a low-pass cutoff frequency of 15 Hz. Instantaneous velocities were computed by differentiating displacement data using a three-point central finite difference algorithm.

Dependent Variables and Statistical Analyses

Movement onset was defined as the frame wherein resultant limb velocity exceeded 50 mm/s for 10 consecutive frames (50 ms), and movement offset was defined as the frame wherein resultant velocity fell below 50 mm/s for the same number of frames. Dependent variables included reaction time (RT, time from the auditory initiation tone to movement onset), movement time (MT, time from movement onset to movement offset), peak velocity (PV, maximum resultant velocity), time after peak velocity (TAPV, time from PV to movement offset), constant error in the primary (CE_p) and secondary (CE_s) movement directions and their associated variable error values (VE_p , VE_s). In addition, we computed spatial correlations (R^2 values) relating the spatial position of the limb at different points in the reaching trajectory to ultimate movement endpoints (primary movement direction only). The logic behind this technique is that reaches controlled more online (i.e., via feedback-based corrections) should produce lower spatial correlations as the unfolding trajectory is modified to attenuate planning errors. In contrast, reaches planned primarily in advance of movement onset should yield more robust spatial correlations as early planning errors unfold without online corrections (see Heath, 2005, for complete details).

In most cases (see exception in the following), data were examined via 2 (response planning: monocular, binocular) by 2 (response control: monocular, binocular) by 2 (limb vision: limb visible, limb occluded) by 2 (target: near, far) fully repeated-measures ANOVA. Where appropriate, F statistics were corrected for violations of sphericity assumption using the appropriate Huynh-Feldt correction (corrected degrees of freedom reported to one decimal place). Simple effects analyses ($\alpha = .05$) were used to decompose interactions. Only significant results are reported ($p < .05$).

Results

The manipulation of monocular and binocular visual signals at response planning did not influence the dependent variables examined here (p values $> .05$; see Table 1 for details). Hence, in the following description of experimental results, monocular and binocular vision refers specifically to visual signals available during response control.

Participants produced their responses with a latency of 202 ± 30 ms, and no manipulation-related RT effects were observed (p values $> .05$). As expected, MT, PV, and TAPV scaled in relation to target eccentricity, $F_s(1, 11) = 55.89, 71.31, 38.43$, respectively, p values $< .001$. In addition, TAPV was longer in the monocular as compared with the binocular visual condition, $F(1, 11) = 5.40, p < .05$ (Table 1).

Monocular reaches undershot target location [CE_p ; $F(1, 11) = 6.37, p < .03$] and showed increased rightward endpoint bias [CE_s ; $F(1, 11) = 10.06, p < .01$] relative to binocular counterparts. What is more, endpoint accuracy in the primary

Table 1 Reaction Time, Movement Time, Peak Velocity, and Time After Peak Velocity as a Function of Monocular and Binocular Viewing Conditions for Trials Performed With and Without Online Limb Vision

Variable	Viewing condition					
	MM	MB	Average	BM	BB	Average
Reaction time (ms)						
limb visible	199 ± 8	203 ± 10	201 ± 8	201 ± 8	204 ± 11	202 ± 9
limb occluded	201 ± 9	203 ± 11	202 ± 10	202 ± 8	211 ± 11	206 ± 9
Movement time (ms)						
limb visible	457 ± 32	455 ± 31	456 ± 30	437 ± 27	455 ± 30	446 ± 27
limb occluded	445 ± 33	460 ± 33	452 ± 32	450 ± 31	455 ± 28	452 ± 28
Peak velocity (mm/s)						
limb visible	1413 ± 166	1470 ± 182	1442 ± 172	1433 ± 169	1432 ± 150	1433 ± 159
limb occluded	1419 ± 167	1478 ± 185	1449 ± 174	1414 ± 177	1389 ± 130	1402 ± 146
Time after peak velocity (ms)						
limb visible	278 ± 24	275 ± 24	277 ± 23	265 ± 21	269 ± 21	267 ± 20
limb occluded	275 ± 23	272 ± 27	273 ± 24	265 ± 23	264 ± 18	264 ± 20

Note. MM = monocular vision during planning and control; MB = monocular vision during planning and binocular vision during control; BM = binocular vision during planning and monocular vision during control; BB = binocular vision during planning and control.

movement direction was optimized when reaches were completed with concurrent binocular cues and online limb vision [i.e., visual signal by limb vision interaction: $F(1, 11) = 9.77, p < .02$]. More specifically, binocular limb-visible reaches were more accurate than limb-occluded counterparts [$t(11) = 2.94, p < .02$], whereas monocular limb-visible and limb-occluded reaches elicited comparable endpoint accuracy [$t(11) = 1.35, p = .20$; Figure 1]. CE_p also revealed an effect of target eccentricity, $F(1, 11) = 9.77, p < .02$; greater undershooting was associated with the far compared with the near target. In terms of endpoint variability, limb-visible trials were more consistent than limb-occluded ones, $F_s(1, 11) = 10.54, 100.31$, respectively, for VE_p and VE_s , p values $< .01$; however, in the primary movement direction, that general effect was influenced by an interaction with monocular and binocular visual signals, $F(1, 11) = 7.64, p < .03$. Endpoints for binocular limb-visible reaches were more stable than limb-occluded counterparts [$t(11) = 4.33, p < .01$], whereas the presence or absence of limb vision did not influence monocular reaches [$t(11) = 1.17, p = .28$; Figure 1].

Figure 2 shows averaged R^2 values relating limb position to ultimate movement endpoints in the primary movement direction as a function of monocular and binocular reaches across limb-visible and limb-occluded trials. From this figure it can be seen that in the latter half of trajectories (i.e., $>50\%$ of MT), binocular reaches performed with concomitant limb vision elicited lower R^2 values than any of the other experimental conditions. To quantify statistically the aforementioned finding, we used a subset of our R^2 values (i.e., 20%, 40%, 60%, 80% of MT) and added this factor (i.e., time) to our ANOVA model. The availability of monocular or binocular vision interacted with time and online limb vision, $F(2.6, 28.2) = 5.00, p < .01$. At 20% and 40% of MT, the different viewing (i.e., monocular and binocular) and limb-vision (limb-visible and limb-occluded) conditions did not influence R^2 values (p values $> .05$). Decomposition of the interaction at 60% and 80% of MT yielded significant main effects for binocular cues [$F_s(1, 11) = 4.95$ and 6.06 , respectively, for 60% and 80% of MT, p values $< .05$] and interactions involving binocular cues and online limb vision [$F_s(1, 11) = 5.05$ and 5.89 , respectively, for 60% and 80% of MT, p values $< .05$]. Binocular reaches elicited lower R^2 values than monocular counterparts. In addition, binocular limb-vision reaches yielded smaller R^2 values than binocular limb-occluded ones (p values $< .05$), whereas monocular limb-visible and limb-occluded reaches elicited comparable R^2 values (p values $> .05$).

Discussion

Binocular Vision Does Not Advantage Movement Planning

Our manipulation of visual cues before movement onset did not influence the reaching movements studied here. Specifically, reaches planned with monocular or binocular vision demonstrated comparable reaction times, peak velocities, and overall movement timing. Analyses of endpoint accuracy and stability further indicated that movement planning processes were not influenced by the presence or absence of binocular vision. What is more, the previously mentioned results held true regardless of whether trials involved matching (i.e., monocular-monocular or

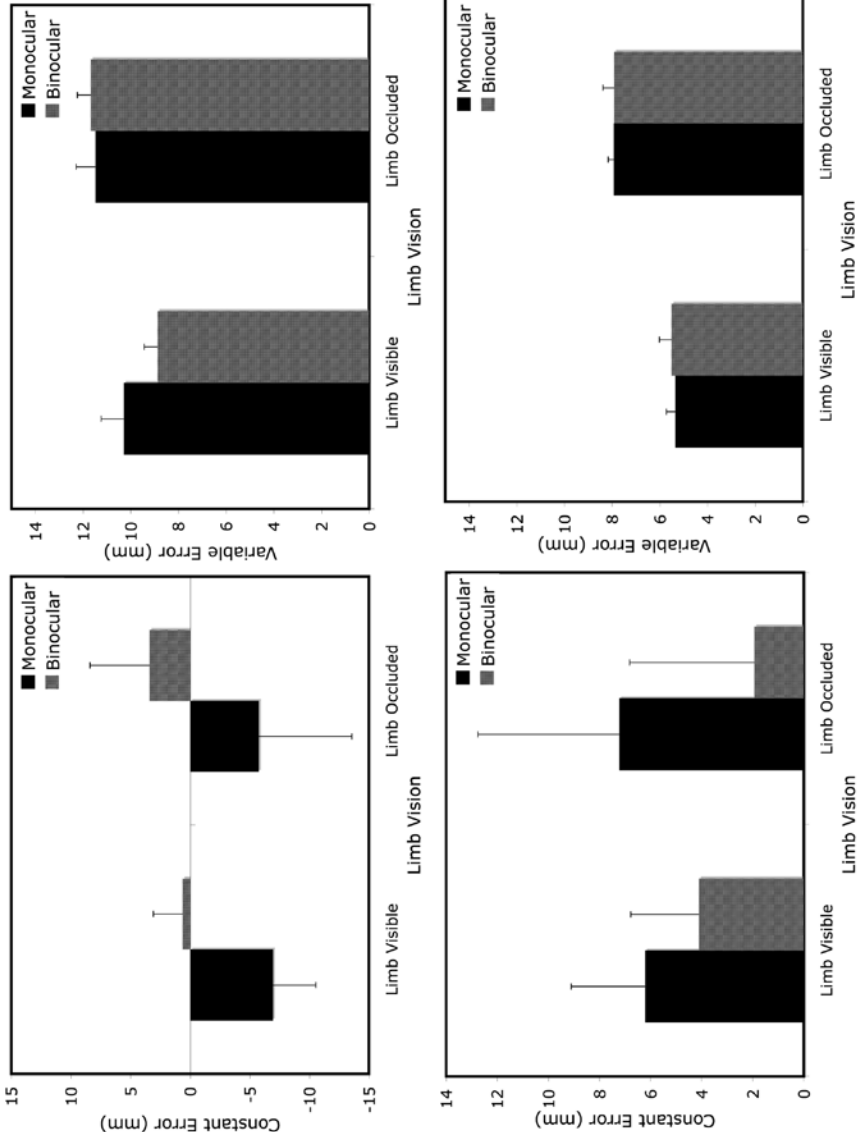


Figure 1 — Constant (mm) and variable (mm) error in the primary (top panels) and secondary (lower panels) movement directions for monocular and binocular reaches during limb-vision and limb-occluded trials. The conditions depicted here reflect the availability of monocular and binocular cues during movement control. Error bars represent between-participant SEM.

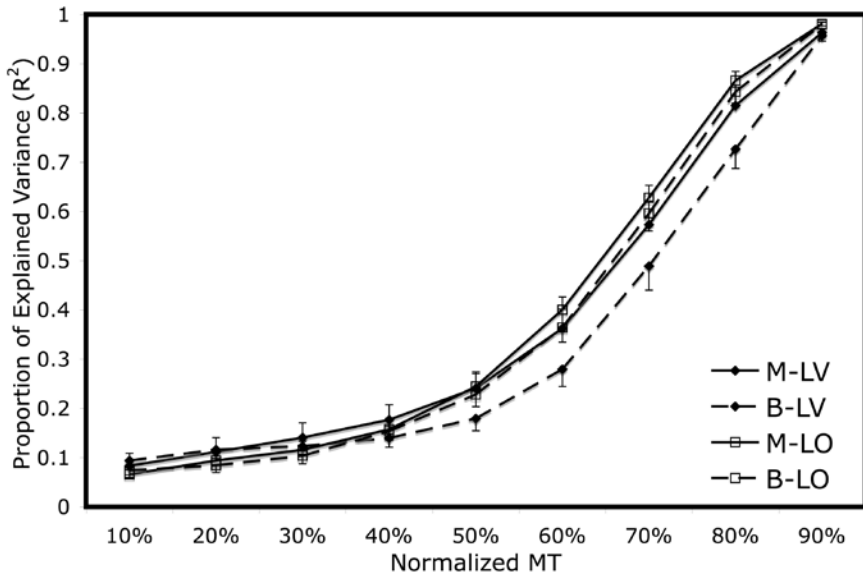


Figure 2 — R^2 values relating the spatial position of the limb at 10% through 90% of normalized movement time (MT) relative to ultimate movement endpoints (primary movement direction). Monocular (M, solid lines) and binocular (B, dashed lines) conditions and their respective limb-visible (LV, closed symbols) and limb-occluded (LO, open symbols) trials are depicted. The conditions depicted here reflect the availability of monocular and binocular cues during movement control. Error bars represent between-participant SEM. Notably, R^2 values at 20%, 40%, 60%, and 80% of MT were submitted to statistical analysis.

binocular-binocular conditions) or counterpart (i.e., monocular-binocular, binocular-monocular conditions) visual cues throughout the planning and control stages, as well as whether vision of the limb was available during to-be-completed responses.² The points just mentioned have particular bearing on the current findings because they suggest that our manipulation of visual cues in advance of movement onset did not produce a strategic difference in the manner participants planned their responses.

Recall that Servos and Goodale (1994) provided the only other investigation designed specifically to disentangle the role of monocular and binocular cues for movement planning and control. In Experiment 1 of their work, an initial binocular view was maintained throughout a response or was altered to a monocular one at movement onset, whereas Experiment 2 provided the opposite manipulation, that is, an initial monocular view was maintained throughout a response or was altered to a binocular one at movement onset. Servos and Goodale report that relative to grasps made with full binocular vision (i.e., binocular-binocular), limb transport dynamics of monocular responses (i.e., monocular-monocular and monocular-binocular) were initiated more slowly and demonstrated reduced peak velocities (cf. Table 1 and Table 2 of that work). In particular, the reduced peak velocities of

monocular-planned actions were taken as evidence of an underestimation of veridical target distance (see also Servos et al., 1992; but see Loftus et al., 2004). It is, however, important to note that statistical comparisons were not made between the performances of the different participants used in Experiments 1 and 2 of Servos and Goodale. In other words, it is not clear from that work whether monocular cues reliably encumber movement planning and the computation of target distance. Of course, in the current investigation, our factorial combination of monocular and binocular viewing during movement planning and control yielded no evidence that monocular vision impairs visuomotor computations associated with early movement kinematics. In particular, our peak velocities show parallel specification of target depth across initial viewing conditions. Notably, such a result is in line with a number of other studies showing that the early kinematics of movement trajectories performed with full monocular or full binocular responses are equivalent (e.g., Bradshaw & Elliott, 2003; Coull et al., 2000; Melmoth & Grant, 2006; Watt & Bradshaw, 2000; Westwood et al., 2005).

An important issue to be addressed is why binocular vision does not reliably advantage movement planning. After all, it is well known that vergence and disparity signals are necessary for the computation of absolute object depth (see Crone, 1992, for historical review). One parsimonious explanation drawn from Glover's (2004) planning/control model is that the initial kinematic parameterization of action is subserved via relative visual cues designed to bring the effector into the vicinity of a target location. During the latter stages of a movement trajectory, however, the planning/control model asserts that online control mechanisms supported via absolute visual information assume command of the unfolding response and are used to implement metrically precise limb corrections (e.g., Glover & Dixon, 2001; see also Heath, Rival, et al., 2004). It is, therefore, entirely possible that the relative goal and nature of the visual information supporting movement planning renders an equivalent pattern of behavior when responses are implemented on the basis of monocular or binocular vision.

Binocular Cues and Online Limb Vision Advantage Feedback-Based Corrections and Response Accuracy During Movement Execution

When binocular vision was available during movement execution, reaches spent less time in movement deceleration and demonstrated increased endpoint accuracy and stability relative to monocular counterparts. Moreover, endpoint accuracy and stability were optimized when participants were provided a binocular view of their moving limb. For monocular reaches, however, accuracy did not benefit from online limb vision. In terms of quantifying whether the just-mentioned results reflect differences in the extent reaches were controlled online versus offline, we computed R^2 values relating the spatial position of the limb at different stages in the reach trajectory relative to ultimate movement endpoints. Results for this analysis mirrored those associated with endpoint accuracy and variability. During the late stage of responses (i.e., >60% of MT), binocular reaches performed with concomitant limb vision produced R^2 values that were lower than the other experimental conditions. Moreover, the timeline in which the R^2 values of binocular limb-vision reaches differed from the other experimental conditions is in keeping with the extant

literature's view that the latter stage of a reach trajectory represents the period wherein visual feedback is used for online limb adjustments (e.g., Woodworth, 1899; see Elliott et al., 2001, for review of this issue). Indeed, earlier work by our group has demonstrated that reaches performed with limb vision produce lower R^2 values relative to limb-occluded counterparts only during the latter half of reach trajectories (Heath, 2005; Heath, Rival, et al., 2004; Heath, Neely, & Binsted, 2007). Similarly, results from a target perturbation paradigm (Krigolson & Heath, 2006) demonstrate that online adjustments (as indexed by R^2 values) to an unexpected change in target location are largely implemented following an initial movement impulse (i.e., during movement deceleration; see also Neely, Tessmer, Binsted, & Heath, 2008).³ Thus, and returning to the current findings, we propose that the reduced spatial correlations of binocular limb-visible reaches late in the trajectory reflect a mode of limb control wherein visual feedback was extensively used to nullify early movement planning errors (i.e., an online mode of control).

A number of previous studies involving reaching and grasping responses have documented that the late kinematics of binocular reaches are more "efficient" than monocular counterparts. For example, Bradshaw and Elliott (2003) reported grasping responses yielded faster deceleration periods under a binocular as compared with a monocular view (see also Servos & Goodale, 1994; Servos et al., 1992), and Loftus and colleagues (2004) reported that a binocular advantage is preferentially expressed when limb and target vision is continuously available to the performer (cf. Westwood et al., 2005). Of course, previous results in combination with those reported here provide strong evidence that the combination of static (vergence, disparities of target location, etc.) and dynamic (stereomotion, diplopic images of the moving limb) cues afforded by binocular vision provide an optimal environment for the implementation of metrical limb/target corrections—a finding in line with Glover's assertion that absolute visual information is preferentially used during the latter stages of movement control.

That binocular reaches unfold primarily online and exhibit accurate and stable movement endpoints relative to monocular counterparts is not surprising because environments affording a rich array of visual cues attenuate visuomotor uncertainty and improve the fidelity of real-time limb corrections (Heath, Rival, & Neely, 2006; Khan, Elliott Coull, Chua, & Lyons, 2002; Zelaznik, Hawkins, & Kisselburgh, 1983). It is, however, important to note that findings from the current investigation do not support the commonly held claim that kinematic and endpoint differences between binocular and monocular reaches reflect a primary reduction in the efficiency of visual feedback used for online corrections in the latter viewing condition. Rather, our results suggest that the adoption of distinct reaching strategies (i.e., online versus offline) underlies important differences in the two viewing conditions. As expressed earlier, the R^2 values and endpoint dynamics of binocular reaches (particularly those paired with online limb vision) are indicative of a primarily online mode of reaching control, whereas matching variables for monocular responses (i.e., increased R^2 values and increased endpoint error) indicate a more offline mode of control. That is not to say that the trajectories of monocular reaches were implemented without online corrections; rather, we believe that the increased visuomotor uncertainty of this viewing environment resulted in the adoption of a mode of control limiting the extent to which visual information was used for feedback-based limb corrections (Heath, Westwood, et al., 2004; Neely

et al., 2008). This conclusion matches a number of other studies demonstrating that visuomotor uncertainty limits the fidelity of online limb corrections and engenders the adoption of a primarily offline mode of movement control (Heath et al., 2006; Krigolson et al., 2007; Schlicht & Schrater, 2007; Trommershauser, Gepshtein, Maloney, Landy, & Banks, 2005; see also Loftus et al., 2004). Indeed, the nature of this more offline mode of control might be related to cost functions limiting the efficiency or effectiveness by which monocular cues can be used for online limb corrections (Knill, 2005). As such, the current investigation offers a new perspective on why monocular responses elicit different endpoint accuracy (for reaching) and object-related metrics (for grasping) relative to binocular counterparts. Specifically, we propose that heightened visuomotor uncertainty under monocular cue conditions results in a mode of control wherein responses are primarily structured in advance of movement onset and unfold without primary use of visual feedback for online limb adjustments.

Conclusions

We believe the current findings add to the visuomotor control literature for three important reasons. First, our findings demonstrate that binocular vision does not provide a unitary benefit to the constituent planning and control stages of action. More specifically, our results suggest that movement planning is a relative goal subserved by relative visual information, whereas movement control represents an absolute goal that is advantaged by the use of binocular cues for online limb corrections. Second, we demonstrate that contemporaneous static and dynamic binocular cues provide a specific enhancement to movement accuracy via the implementation of effective online corrections. Third, we provide primary evidence to suggest that differences in the control of monocular and binocular reaches reflect the former condition's use of a more offline mode of control to account for increased visuomotor uncertainty and reduced fidelity of visual information for feedback-based corrections.

Notes

1. Servos et al.'s (1992, see also Servos, 2000) report that grip apertures are smaller under monocular as compared with binocular viewing conditions represents an atypical finding in the grasping literature. Indeed, most work indicates that a reduction or loss in visual cues elicits a "play it safe" mode of control wherein larger grip apertures are formulated to account for increased visuomotor uncertainty (Jakobson & Goodale, 1991; Schlicht & Schrater, 2007; Sivak & MacKenzie, 1990; Wing, Turton, & Fraser, 1986).
2. Limb vision was always available to participants during movement planning so that the premovement calibration of limb position was equivalent across limb-visible and limb-occluded trials (Prablanc, Echallier, Jeannerod, & Komilis, 1979).
3. R^2 values early in the reach trajectory are thought to be insensitive to visuomotor uncertainty because at this stage of the response, the spatiotemporal features of the initial movement impulse have not had sufficient time to unfold (e.g., Heath, Rival, et al., 2004).

Acknowledgments

This research was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant and a University of Western Ontario Major Academic Fund Award (MH).

References

- Bradshaw, M.F., & Elliott, K.M. (2003). The role of binocular information in the “on-line” control of prehension. *Spatial Vision, 16*, 295–309.
- Bradshaw, M.F., Elliott, K.M., Watt, S.J., Hibbard, P.B., Davies, I.R.L., & Simpson, P.J. (2004). Binocular cues and the control of prehension. *Spatial Vision, 17*, 95–110.
- Bryden, M.P. (1977). Measuring handedness with questionnaires. *Neuropsychologia, 15*, 617–624.
- Coull, J., Weir, P.L., Tremblay, L., Weeks, D.J., & Elliott, D. (2000). Monocular and binocular vision in the control of goal-directed movement. *Journal of Motor Behavior, 32*, 347–360.
- Crone, R.A. (1992). The history of stereoscopy. *Documenta Ophthalmologica, 81*, 1–16.
- 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.
- Glover, S. (2004). Separate visual representations in the planning and control of action. *The Behavioral and Brain Sciences, 27*, 3–78.
- Glover, S., & Dixon, P. (2001). Motor adaptation to an optical illusion. *Experimental Brain Research, 137*, 254–258.
- Heath, M. (2005). Role of limb and target vision in the online control of memory-guided reaches. *Motor Control, 9*, 281–311.
- Heath, M., & Binsted, G. (2007). Visuomotor memory for target location in near and far reaching spaces. *Journal of Motor Behavior, 39*, 169–177.
- Heath, M., Neely, K., & Binsted, G. (2007). Allocentric visual cues influence online limb adjustments. *Motor Control, 11*, 54–70.
- Heath, M., Rival, C., & Binsted, G. (2004). Can the motor system resolve a premovement bias in grip aperture? Online analysis of grasping the Müller-Lyer illusion. *Experimental Brain Research, 158*, 378–384.
- Heath, M., Rival, C., & Neely, K. (2006). Visual feedback schedules influence visuomotor resistance to the Müller-Lyer figures. *Experimental Brain Research, 168*, 348–356.
- Heath, M., & Westwood, D.A. (2003). Can 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., & Binsted, G. (2004). 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.
- Jakobson, L.S., & Goodale, M.A. (1991). Factors affecting higher-order movement planning: A kinematic analysis of human prehension. *Experimental Brain Research, 86*, 199–208.
- 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.

- Knill, D.C. (2005). Reaching for visual cues to depth: The brain combines depth cues differently for motor control and perception. *Journal of Vision*, *5*, 103–115.
- Krigolson, O., Clark, N., Heath, M., & Binsted, G. (2007). The proximity of visual landmarks impacts reaching performance. *Spatial Vision*, *20*, 317–336.
- Krigolson, O., & Heath, M. (2004). Background visual cues and memory-guided reaching. *Human Movement Science*, *23*, 861–877.
- Krigolson, O., & Heath, M. (2006). A lower visual field advantage for endpoint stability but no advantage for online movement precision. *Experimental Brain Research*, *170*, 127–135.
- Loftus, A., Servos, P., Goodale, M.A., Mendarozqueta, N., & Mon-Williams, M. (2004). When two eyes are better than one in prehension: Monocular viewing and end-point variance. *Experimental Brain Research*, *158*, 317–327.
- Marotta, J.J., Behrmann, M., & Goodale, M.A. (1997). The removal of binocular cues disrupts the calibration of grasping in patients with visual form agnosia. *Experimental Brain Research*, *116*, 113–121.
- Melmoth, D.R., & Grant, S. (2006). Advantages of binocular vision for the control of reaching and grasping. *Experimental Brain Research*, *171*, 371–388.
- Miles, W.R. (1930). Ocular dominance in human adults. *The Journal of General Psychology*, *3*, 412–420.
- Neely, K.A., Tessmer, A., Binsted, G., & Heath, M. (2008). Goal-directed reaching: Movement strategies influence the weighting of allocentric and egocentric visual cues. *Experimental Brain Research*, *186*, 375–384.
- 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.
- Previc, F.H. (1998). The neuropsychology of 3-D space. *Psychological Bulletin*, *124*, 123–164.
- Schlicht, E.J., & Schrater, P.R. (2007). Effects of visual uncertainty on grasping movements. *Experimental Brain Research*, *182*, 47–57.
- Servos, P. (2000). Distance estimation in the visual and visuomotor systems. *Experimental Brain Research*, *130*, 35–47.
- Servos, P., & Goodale, M.A. (1994). Binocular vision and the on-line control of human prehension. *Experimental Brain Research*, *98*, 119–127.
- Servos, P., Goodale, M.A., & Jakobson, L.S. (1992). The role of binocular vision in prehension: A kinematic analysis. *Vision Research*, *32*, 1513–1521.
- Sivak, B., & MacKenzie, C.L. (1990). Integration of visual information and motor output in reaching and grasping: The contributions of peripheral and central vision. *Neuropsychologia*, *28*, 1095–1116.
- Trommershauser, J., Gepshtein, S., Maloney, L.T., Landy, M.S., & Banks, M.S. (2005). Optimal compensation for changes in task-relevant movement variability. *The Journal of Neuroscience*, *25*, 7169–7178.
- Watt, S.J., & Bradshaw, M.F. (2000). Binocular cues are important in controlling the grasp but not the reach in natural prehension movements. *Neuropsychologia*, *38*, 1473–1481.
- Westwood, D.A., Robertson, C., & Heath, M. (2005). Action control: Independent effects of memory and monocular viewing on reaching accuracy. *Brain and Cognition*, *57*, 257–260.
- Wing, A.M., Turton, A., & Fraser, C. (1986). Grasp size and accuracy of approach in reaching. *Journal of Motor Behavior*, *18*, 245–260.
- Woodworth, R.S. (1899). The accuracy of voluntary movement. *Psychological Review*, *3*, 1–114.
- Zelaznik, H., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior*, *15*, 217–236.