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Abstract

We sought to determine whether a putative lower-visual field (loVF) advantage for projections to the visuomotor networks of the dorsal visual pathway influences online reaching control.

Participants reached to 3D depth targets presented in the loVF and upper-visual field (i.e., upVF) in binocular and monocular visual conditions, and when online vision was available (i.e., closed-loop: CL) or unavailable (i.e., open-loop: OL). To examine the degree responses were controlled online we computed the proportion of variance (R^2) explained by the spatial position of the limb at distinct stages in the reaching trajectory relative to a response's ultimate movement endpoint.

Results showed that binocular and CL reaches exhibited shorter movement times and more online corrections (i.e., smaller R^2 values) than their monocular or OL counterparts. Notably, however, loVF and upVF reaches exhibited equivalent performance metrics across all experimental conditions. Accordingly, results provide no evidence of a loVF advantage for online control.

Keywords: *asymmetry; binocular; lower-visual field; monocular; reaching; retina*

1 **Introduction**

2 The horizontal meridian of the human retina has an increased density of ganglion cells in the
3 central (i.e., foveal) than the peripheral retina (Curcio, Sloan, Packer, Hendrickson, Kalina,
4 1987). The functional consequence of this well-documented asymmetry is increased resolution
5 power for stimuli appearing in foveal vision. A less well-known asymmetry exists in the vertical
6 meridian with an increased density of retinal ganglion cells in the superior as compared to the
7 inferior hemiretina (Curcio & Allen, 1990). Given the concave surface of the retina, the superior
8 and inferior hemiretina receive visual information from the lower- (i.e., loVF) and upper-visual
9 fields (i.e., upVF), respectively. Previc's (1990) theoretical account of primate visual space
10 asserts a loVF advantage for goal-directed actions, and an upVF advantage for object search and
11 perception-based processing. Moreover, Danckert and Goodale (2003) contend that the loVF
12 advantage for action is not purely 'retinal' in nature, but also reflects preferential inputs from the
13 loVF to the visuomotor networks of the dorsal visual pathway. In contrast, the upVF is
14 proposed to be biased toward the processing of cognitive-based information due to direct inputs
15 to the visuoperceptual networks of the ventral visual pathway.

16 Danckert and Goodale (2001) provided the first systematic examination of the
17 behavioural consequence of a vertical visual field asymmetry. In that work, participants
18 performed a Fitts (1954) reciprocal tapping task (index of difficulty (ID): values ranging from
19 0.3 to 1.5 bits of information) to targets located in the loVF and upVF. To manipulate the visual
20 field, participants fixated a location above or below the target so that it appeared in their loVF or
21 upVF, respectively – an elegant manipulation that also equated reaches for biomechanical
22 constraints. Movement times (MT) for loVF reaches adhered to lawful speed-accuracy relations,
23 whereas MTs for upVF reaches did not vary with ID and were less accurate than loVF reaches.

1 Accordingly, the authors proposed a functional loVF advantage for visually guided actions (see
2 also Khan & Lawrence, 2005). In addition, Rossit and colleagues (Rossit, McAdam, McLean,
3 Goodale, & Culham, 2013) employed a conjoint grasping and fMRI study to examine the neural
4 correlates associated with the loVF advantage. Rossit et al.'s behavioural findings indicated that
5 grasping movements in the loVF exhibited more veridical scaling to target size and produced less
6 variability than their upVF counterparts. As well, fMRI findings indicated that loVF grasps were
7 linked to increased activation of the superior parieto-occipital cortex (SPOC) and left precuneus
8 (brain regions linked to the control of reaching), and that no such visual field effect was observed
9 during a passive viewing condition.

10 It is important to recognize that work has not consistently reported a loVF advantage for
11 speed-accuracy relations in goal-directed actions. Binsted and Heath (2005) had participants
12 complete reaches across a wider range of IDs (i.e., 1.5 to 5.5 bits) than Danckert and Goodale
13 (2001). The basis for including a broader range of IDs was twofold. First, Danckert and
14 Goodale employed IDs that were not within the range that Fitts (Fitts, 1954; Fitts & Peterson,
15 1964) and more contemporary research has shown to produce speed-accuracy trade-offs (for
16 review see Heath, Weiler, Marriott, Elliott, & Binsted, 2011). Second, the *very* low IDs used by
17 Danckert and Goodale would have entailed reaches specified entirely offline via central planning
18 mechanisms (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979), and would therefore not
19 gauge a possible loVF advantage for online control. As such, the IDs employed by Binsted and
20 Heath entailed movement environments that spanned reaches controlled primarily via central
21 planning mechanisms (i.e., ID = 1.5 bits) and those requiring online trajectory amendments (i.e.,
22 ID = 5.5 bits). Results showed that loVF and upVF reaches elicited comparable MT/ID slopes,
23 time in the online correction phase of the response (i.e., time after peak velocity), and endpoint

1 accuracy. The only identified difference was that the loVF elicited less variable endpoints.
2 These findings were attributed to: (1) a practice/learning effect for loVF reaches, and/or (2) a
3 modest loVF advantage associated with the planning – but not the online control – of reaches
4 (see also Brown, Halpert, & Goodale, 2005). In another study, Krigolson and Heath (2006)
5 employed a target ‘jump’ at movement onset to determine whether online corrections in the loVF
6 produce shorter latencies than upVF reaches. Results showed that loVF reaches elicited
7 decreased endpoint variability (across ‘jump’ and ‘no-jump’ trials) but did not demonstrate an
8 increased rate or effectiveness in online corrections. Once again, such results provide some
9 evidence of a loVF advantage for movement planning but not online control.

10 An identified feature of the dorsal stream is the processing of visual information at the
11 time of response cuing (i.e., real-time control) (Westwood & Goodale, 2003) and continuously
12 during response execution (Pisella et al., 2000; for review see Goodale, 2011) – a control mode
13 ensuring that the visual system continuously updates the absolute position of the effector and
14 target. As such, the present investigation had participants complete loVF and upVF reaches in
15 conditions that manipulated the availability of visual cues during movement planning and
16 control. Participants completed goal-directed reaches wherein visual input was selectively
17 available during movement planning (i.e., open-loop: OL) or available during movement
18 planning and execution (i.e., closed-loop: CL). Furthermore, CL and OL trials were performed
19 in binocular and monocular conditions because binocular signals provide the motor system with
20 distinct advantages for movement planning and control. For example, accurate distance control
21 *for movement planning* is supported by the vergence angle between the two eyes when bi-
22 fixating a target (Brenner and Van Damme 1998; Tresilian, Mon-Williams & Kelly 1999). In
23 *online control* is optimized by binocular signals related to the reduction in image size of the

viewer's hand as it approaches a target object (Melmoth and Grant 2006; Servos and Goodale 1994). In contrast, removing binocular signals results in the reliance on monocular cues such as texture, illumination, perspective, and contextual information – cues that do not optimize movement planning or control (Previc 1998). Evidence has shown that binocular cues are necessary for the normal operation of the dorsal visual pathway, and that reaches performed in a monocular environment may be mediated via the ventral visual pathway (Marrotta, Behrmann, & Goodale, 1997). In addition, it has been shown that binocular and monocular reaches are mediated via distinct control strategies (i.e., online vs. offline). Heath, Neely, & Krigolson (2008) had participants complete binocular and monocular reaches to computer-generated targets located at different eccentricities in the depth plane and quantified online correction via regression analyses that examined the relationship between the spatial location of the limb at decile increments of normalized MT relative to a response's movement endpoint (i.e., R^2 values). The basis for this technique is that reaches controlled primarily online exhibit weak R^2 values at later stages in the trajectory as the unfolding response evokes error-reducing trajectory amendments. In turn, more robust R^2 values are taken to evince a trajectory that is structured offline via central planning mechanisms (for review see Heath, Neely, Krigolson, & Binsted, 2010). Results showed that binocular reaches produced weaker R^2 values (i.e., at $> 50\%$ of MT) and more accurate, less variable endpoints than monocular reaches – a result taken to evince that binocular visual cues advantage an online mode of control (see also Hu & Knill, 2011).

The present work examined whether the presence/absence of binocular cues in CL and OL environments differentially influences the putative loVF advantage for reaching. As in previous work, participants fixated above or below a target object to manipulate the visual field in which it was presented and completed binocular and monocular reaches in CL or OL visual

environments. Moreover, previous work contrasting loVF and upVF reaches has employed 2D targets (i.e., a computer image or LED embedded in a stimulus board), whereas we presented 3D targets that varied in depth from a stimulus board. This represents an important manipulation as work has shown that the binocular superiority in reaching manifests in conditions involving a 3D target (Coull, Weir, Tremblay, Weeks, & Elliott, 2000). Accordingly, if a loVF advantage manifests for online control then the magnitude of such an advantage may be greatest when interacting with a 3D target. In terms of research predictions, if the loVF elicits an advantage for online control then such actions performed with binocular cues and in a CL environment should produce shorter MTs and lower R^2 values than their upVF counterpart. If, however, loVF reaches performed with binocular cues in both CL *and* OL environments show equivalent MTs and R^2 values that are more efficient and effective than their upVF counterparts then results would demonstrate a loVF advantage for movement planning. As a third alternative, it is possible that the anatomical asymmetry in the vertical retinal axis and the proposed preferential access to dorsal visuomotor networks does not produce a behavioural advantage in the planning or online control of reaches.

Methods

Participants

A group of fifteen participants (12 female: age range = 18 – 36 years) completed CL reaches, and a separate group of fourteen participants (12 female: age range = 19 – 27 years) completed OL reaches. We employed a between-groups design due to the duration of individual CL and OL experimental sessions (i.e., 90 minutes). All participants were right handed according to the Edinburgh Handedness Questionnaire (Oldfield, 1971), and had normal or corrected-to-normal vision. Eye dominance was tested using the Hole-in-Card Test, and the participants' non-

dominant eye was occluded during the monocular condition (Johansson, Seimyr, & Pansell, 2015). All participants had stereoacuties of 120" of arc or better using the TNO test for stereoscopic vision (Walraven, 1972), and values for the CL (35", SD = 12) and OL (43", SD = 33), groups did not reliably differ ($t(22) = 1.64, p > 0.05$)¹. Participants signed consent forms approved by the institutional ethics committee of the University of East Anglia and the Non-Medical Research Ethics Board, University of Western Ontario. All work was conducted in accordance with the Declaration of Helsinki.

Apparatus and Procedures

Participants sat at a table (height = 800 mm) with their head placed in a chin rest located 300 mm from the table. A start button was positioned on the table top at the participants' midline and 420 mm from a stimulus board. Targets were affixed to a stimulus board (centred at participants' midline) 550 mm in front of participants with targets located 450 mm in height (i.e., Y-axis) from the table top surface. Reaches with the right hand were directed to each of three 3D targets (20 mm by 20 mm cube) located at the following depths (i.e., Z-axis): 253 mm (i.e., proximal), 192 mm (i.e., middle), and 53 mm (i.e., distal) from the anterior surface of the stimulus board. As a result, reaches to the proximal, middle and distal targets required 167 mm, 228 mm and 367 mm of depth displacement, respectively from the start button. A white LED 10 mm in diameter was located on the face of each target and was illuminated for the duration of a trial. Two red fixation LEDs 150 mm (16° visual angle) above and below the target were used to manipulate the visual field a target was presented (**Figure 1**). In particular, gaze directed to the fixation LEDs above and below the target resulted in a target presented in the loVF and upVF, respectively. Participants wore liquid-crystal shutter-goggles (PLATO, Translucent Technologies, Toronto, ON, Canada) and a Qualisys Oqus (Qualisys AB, Sweden) sampling at 179 Hz measured the

1 position of a small passive marker affixed to the posterior surface of participants' right index
2 finger. The lights in the laboratory were dimmed to ensure appropriate vision of all LEDs while
3 reducing background visual cues.

4 A trial began with the goggles set to their translucent state while the experimenter placed
5 a target on the stimulus board. Following this, and once the participant pressed the start button
6 with their right index finger, the goggles became transparent and the participant was instructed to
7 direct (and maintain) their gaze on the illuminated fixation LED. After a 2,000 ms fixation
8 foreperiod, the target was illuminated simultaneously with a tone that instructed the participant to
9 reach "quickly and accurately" with their right hand to touch the centre of the target LED.

10 Separate groups of participants completed their reaches in CL and OL environments. In the CL
11 group, the goggles remained transparent during movement planning and execution and vision
12 was occluded only after movement offset (see kinematic definition of movement offset below).
13 Accordingly, participants were able to maintain their gaze on the illuminated fixation LED for
14 the duration of a trial. In contrast, for the OL group the goggles were set to their translucent state
15 coincident with the release of the start button, and as a result, participants were instructed to
16 maintain their gaze on the remembered location of the fixation LED for the duration of a trial.

17 CL and OL groups completed their reaches in two stereo-cue conditions (i.e., monocular and
18 binocular). During the binocular condition the goggles provided vision through both lenses
19 during response planning (i.e., CL and OL) and control (i.e., CL). In the monocular condition,
20 only the lens associated with participants' dominant eye was transparent during response
21 planning (i.e., CL and OL) and control (i.e., CL). Each visual field by stereo-cue condition
22 combination contained 50 trials (i.e., 10 trials to the distal target, 30 trials to the middle target,
23 and 10 trials to the proximal target). The presented study analyzed only reaches to the more

frequent middle target and included the distal and proximal targets as foils to prevent stereotyped actions and to require the trial-to-trial processing of target-based depth cues. Monocular and binocular reaches were completed in separate blocks and within each block the three target positions and visual field presentations (i.e., loVF, upVF) were pseudo-randomized. Last for the CL condition, participants completed a simultaneous fixation task to ensure that they remained fixated for the entirety of a trial. The fixation task included 0, 1, or 2 flashes of the fixation LED that the participant reported to the experimenter at the end of the trial. The fixation flashes occurred before and during the movement to ensure that the target remained in the appropriate visual field for response duration. A trial involving a fixation task error was deleted and re-entered into the trial matrix (i.e., <6% of trials). All CL trials analyzed here entailed fixation in the appropriate visual field. Of course, a fixation task was not possible for the OL condition given that the goggles were set to the translucent state during movement execution. Notably, however, the performance of the fixation task during the CL condition indicated that participants did not have difficulty in maintaining task-based fixation instructions.

As noted above, in the CL group the goggles were set to their translucent state coincident with movement offset (see details below) – a manipulation that was done to equate CL and OL groups for the absence of offline visual feedback (for review of offline visual feedback, see Khan et al. 2006). The movement offset criterion was defined via an offline kinematic measure that resulted in the goggles being set to their translucent state approximately 85 ms after participants' finger contacted the target. As such, participants in the CL group were provided – albeit briefly – a limited sample of offline feedback.

Data Acquisition and Analysis

Position data of the marker affixed to the index finger were filtered via a dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Movement onset was determined by release of the start button and movement offset was marked when velocity was less than 50 mm/s for 15 consecutive frames. Dependent measures included: reaction time (RT: time from auditory imperative to movement onset), movement time (MT: time from movement onset to movement offset), percent time after peak velocity (%TAPV: the % of MT between peak velocity (PV) and movement offset), and variable error in direction (VE_X), distance (VE_Y) and depth (VE_Z) movement axes. The proportion of endpoint variance (R^2) explained by the spatial position of the limb at proportional increments of MT (20%, 40%, 60%, and 80% of MT) relative to each response's ultimate movement endpoint was computed for each movement axis (i.e., R^2_X , R^2_Y and R^2_Z). Previous work has shown that small and large R^2 values indicate on- and offline modes of control, respectively (Heath, 2005). **Figure 2** presents the spatial correlations for an exemplar participant to demonstrate the computation of R^2 values in the depth axis and shows that binocular reaches were associated with smaller R^2 values (i.e., controlled online) than their monocular counterparts.

Five participants (4 from the CL and 1 from the OL group) were removed due to equipment error (i.e., the index finger marker was only intermittently tracked). Most dependent variables were analyzed via 2 (feedback group: CL vs. OL) by 2 (stereo-cue: binocular vs. monocular) by 2 (visual field: loVF vs. upVF) split-plot ANOVAs. For the R^2 analyses, the variable time (20%, 40%, 60%, 80% of MT) was added to the ANOVA model. Significant effects/interaction were identified via an alpha level of 0.05 or less. Power polynomials (Pedhazur, 1997) and simple effects were used to decompose main effects and interactions. Furthermore, only trials landing on the target (i.e., a “hit”) were captured in this study; that is, a

target wherein the finger did not land on the target (i.e., a “miss”) were discarded and re-entered into the trial matrix. This criterion resulted in less than 4% of trials for any participant being discarded and re-run, and the low percentage of miss trials is perhaps not a surprising finding given the movement times associated with the present work (see details below).²

Results

Performance and kinematic variables

The grand mean for RT was 407 ms (SD = 56) and this variable did not elicit significant main effects or interactions, all $F(1,22) < 1.39$, $ps > 0.29$, all $\eta_p^2 < 0.06$. For MT and %TAPV, results yielded main effects of stereo-cue, all $F(1,22) = 27.13$ and 21.02 , $ps < 0.01$, $\eta_p^2 = 0.55$ and 0.49 for MT and %TAPV, respectively. For binocular trials, MTs (614 ms, SD = 107) and %TAPV (73% SD = 5) were less than their monocular counterparts (MT: 674 ms, SD = 117; %TAPV: 76% SD = 3). Further, MT yielded a main effect of feedback group, $F(1,22) = 15.03$, $p < 0.01$, $\eta_p^2 = 0.41$, and a feedback group by stereo-cue interaction, $F(1,22) = 4.62$, $p < 0.05$, $\eta_p^2 = 0.17$. MTs for CL binocular (529 ms, SD = 61) and monocular (616 ms, SD = 86) trials were shorter than their OL counterparts (binocular: 695 ms, SD = 97, monocular: 720, ms SD = 111), ($ts(22) > 2.51$, $ps < 0.05$). More notably, **Figure 3** demonstrates that the nature of the interaction is rooted in the fact that CL binocular trials yielded shorter MTs than the remaining experimental conditions. Further, and because of the primary objective of this study, we note that MT and %TAPV did not produce main effects of visual field nor any higher-order interactions involving visual field, all $F(1,22) < 1.31$, $ps > 0.26$, all $\eta_p^2 < 0.06$.

VE_X produced a main effect of feedback group, $F(1,22) = 11.71$, $p < 0.01$, $\eta_p^2 = 0.35$: endpoints were less variable for the CL (5.9 mm, SD = 1.6) than OL (10.8 mm, SD = 7.7) group. VE_X did not produce a reliable effect for visual field nor any higher-order interaction involving

visual field, $F(1,22) < 1.20$, $ps > 0.28$, $\eta_p^2 < 0.05$. In terms of VE_Y , results did not elicit any reliable main effects, all $F(1,22) < 1.98$, $ps > 0.17$, $\eta_p^2 < 0.10$; however, we did observe a feedback group by stereo-cue by visual field interaction that approached conventional levels of significance, $F(1,22) = 3.88$, $p = 0.062$, $\eta_p^2 = 0.15$. Notably, however, even when decomposing the interaction via unprotected t-tests, it was found that loVF and upVF trials did not reliably differ in either binocular or monocular conditions, and was a result consistent across CL and OL groups (CL group: all $t(10) < 1.78$, $ps > 0.14$; OL group: all $t(12) < 1.84$, $ps > 0.10$) (**Figure 4**). In other words, results did not demonstrate a difference between loVF and upVF trials across matched stereo-cue and feedback group manipulation. Results for VE_Z produced an effect for feedback group, $F(1,22) = 7.09$, $p < 0.02$, $\eta_p^2 = 0.24$, such that endpoints were less variable for the CL (8.0 mm, SD = 1.8) than OL (17.6 mm, SD = 22.4) group. Last, VE_Z did not produce a reliable effect for visual field nor any higher-order interaction involving visual field, $F(1,22) < 1.54$, $ps > 0.22$, $\eta_p^2 < 0.06$.

Spatial correlations (R^2) in reaching trajectories

R^2_x elicited a main effect of time, $F(3,66) = 92.79$, $p < 0.01$, $\eta_p^2 = 0.81$, and feedback group, $F(1,22) = 18.63$, $p < 0.01$, $\eta_p^2 = 0.46$, and interactions involving time by feedback group, $F(3,66) = 19.46$, $p < 0.01$, $\eta_p^2 = 0.47$, and time by stereo-cue, $F(3,66) = 3.32$, $p < 0.01$, $\eta_p^2 = 0.13$. For CL and OL groups, R^2_x values increased linearly with increasing MT (only linear effects significant: CL $F(1,10) = 29.79$, $p < 0.01$; OL $F(1,12) = 157.20$, $p < 0.01$). Further, CL and OL groups exhibited equivalent R^2_x values at 20% and 40% of MT (all $t(22) < 1.20$, $ps > 0.25$); however, at 60% and 80% MT, R^2_x values for the CL group were smaller than the OL group (all $t(22) = 3.34$ and 5.61 , $ps < 0.01$) (**Figure 5**). For the time by stereo-cue interaction, results showed that values for binocular and monocular conditions increased linearly with MT

(only linear effect significant: all $F(1,22) = 82.01$ and 167.08 , $ps < 0.001$). Further, values for binocular and monocular conditions did not differ from 20% to 60% of MT (all $t(22) < 2.01$, $ps > 0.06$); however, at 80% of MT R^2_X values in the former were smaller ($t(22) = 2.15$, $p < 0.05$ (**Figure 5**). Notably, neither a main effect of visual field nor any higher-order interactions involving visual field were observed, all $F(1,22)$ or $(3,66) < 1.18$, $ps > 0.36$, all $\eta_p^2 < 0.05$.

R^2_Y elicited a main effect of time, $F(3,66) = 28.14$, $p < 0.01$, $\eta_p^2 = 0.56$: values increased linearly with increasing MT (only linear effects significant: CL $F(1,10) = 10.48$, $p < 0.01$; OL $F(1,12) = 20.31$, $p < 0.01$). Notably, neither a main effect of visual field nor any higher-order interactions involving visual field were observed, all $F(1,22)$ or $(3,66) < 2.18$, $ps > 0.10$, all $\eta_p^2 < 0.09$ (see **Figure 5**).

R^2_Z elicited main effects of time, $F(3,66) = 21.70$, $p < 0.01$, $\eta_p^2 = 0.50$, feedback group, $F(1,22) = 7.49$, $p < 0.05$, $\eta_p^2 = 0.25$, and stereo-cue, $F(1,22) = 16.35$, $p < 0.01$, $\eta_p^2 = 0.43$, and a time by feedback group interaction, $F(3,66) = 5.26$, $p < 0.01$, $\eta_p^2 = 0.19$. **Figure 5** shows that R^2_Z values for the CL group were lower than the OL group, and that values were lower for the binocular than the monocular condition. In terms of the time by feedback group interaction, CL and OL groups exhibited equivalent R^2_Z values at 20%, 40%, and 60% of MT (all $t(22) < 1.46$, $ps > 0.16$); however, at 80% of MT values for the CL group were less than the OL group ($t(22) = 3.04$, $p < 0.05$). Notably, neither a main effect of visual field nor any higher-order interactions involving visual field were observed, all $F(1,22)$ and $(3,66) < 0.43$, $ps > 0.73$, all $\eta_p^2 < 0.02$.

Discussion

The present investigation sought to: (1) determine whether the availability of binocular vision affects the proposed loVF advantage for goal-directed reaching, and (2) examine whether a putative loVF advantage is related to enhanced movement planning and/or online control (i.e.,

CL vs. OL groups). Before turning to our primary objectives, we first discuss the general differences associated with the stereo-cue and visual feedback manipulations used here.

Binocular versus monocular reaches

Binocular and monocular reaches produced equivalent endpoint variability; however, the former were associated with shorter MTs, reduced %TAPV, and lower R^2 values in the direction and depth axes (see also Heath et al., 2008; Hu & Knill, 2011; Marotta et al., 1997; Servos, Goodale, & Jakobson, 1992; Servos & Goodale, 1994). Thus, and although similar in endpoint metrics, binocular reaches were more efficient than their monocular counterparts. Moreover, because the deceleration phase represents the time wherein participants implement trajectory corrections (for review see Elliott, Helsen, & Chua, 2001), the %TAPV and directional R^2 values for binocular reaches is taken to evince that stereoptic cues afforded an online mode of control supported via the ‘fast’ visuomotor networks of the dorsal visual pathway (Dijkerman & Milner, 1998; Dijkerman, Milner, & Carey, 1996; Marotta et al., 1997). In turn, the monocular findings are in line with evidence that such actions are associated with decreased online control and implemented, in part, via the ‘slow’ visuoperceptual networks of the ventral visual pathway (Heath et al. 2008; Rossetti et al., 2005).

Previous work has reported that binocular reaches are more accurate and less variable than their monocular counterparts (e.g., Heath et al., 2008; Hu & Knill, 2011). As such, an important issue to address is why the current study observed equivalent endpoint variability in the different stereo-cue conditions. One possible reason is that previous work presented computer-generated targets. Hu and Knill (2011) reported that the absence of penumbrae surrounding a computer-generated image results in ‘distrust’ of monocular visual information and renders decreased certainty (and increased noise) related to target location. Of course, in the

present study target penumbrae were equated across monocular and binocular conditions. A second possibility is that computer-generated images permit responses to be completed without the need for the effector to land *within* the target boundary (e.g., Heath et al. 2008); that is, the participant (and not the target's physical boundary) determines the tolerance for an acceptable level of endpoint precision. In contrast, the current study employed 3D targets in the picture plane (surface of 20 mm by 20 mm) that were disparate in depth from the stimulus board – a manipulation used to increase participants' reliance on depth cues. As a result, participants were required to place their finger on the target's physical surface to complete their response and therefore decreased the potential for between-condition differences in endpoint metrics. In support of this view, the present work found that monocular reaches produced longer MTs than their binocular counterparts are were associated with reduced online control. Accordingly, the present study provides a framework for determining whether an environment fostering a primarily online mode of control (i.e., binocular condition) differentially influences loVF and upVF reaches.

Closed-loop versus open-loop reaches

The CL group had shorter MTs and less variable endpoints (direction and depth axes) than the OL group, and the former produced lower R^2 values (direction and depth axes) during the later stages of the response (i.e., > 60% of MT). Moreover, the CL group's binocular MTs were shorter than any of the other experimental conditions. Regarding, the general difference between CL and OL groups, our results are consistent with studies demonstrating that continuous limb and target vision provides the sensorimotor environment optimizing online corrections (for review see Heath et al., 2010). In contrast, removing limb and target vision (i.e., OL group) has been shown to result in the adoption of a primarily offline mode of control and decreased

1 reaching efficiency and effectiveness (Heath, 2005; Heath, Westwood, & Binsted, 2004; Meyer,
2 Abrams, Kornblum, Wright, & Smith, 1988; Schmidt et al., 1979). Further, that the MTs for the
3 CL group were shortest during the binocular condition indicates that online corrections specified
4 via binocular cues provided the optimal environment for reaching efficiency. This result
5 demonstrates that CL binocular reaches provide a framework for determining whether the
6 optimal environment for reaching efficiency is influenced by the visual field (i.e., loVF vs.
7 upVF) a target is presented.

8 *No evidence for a loVF advantage in the planning or online control of goal-directed reaches*

9 Some work has reported that loVF reaches produce advantaged speed-accuracy relations
10 (Danckert & Goodale, 2001) and online trajectory amendments (Khan & Lawrence, 2005),
11 whereas other work has not (Binsted & Heath, 2005; Krigolson & Heath, 2006). In the present
12 study, loVF and upVF MT, %TAPV, VE_x , VE_z , and all R^2 values did not reliably differ. In fact,
13 VE_y was the only metric that exhibited a potential difference between loVF and upVF trials, as it
14 was associated with a feedback group by stereo-cue by visual field interaction that *approached* a
15 conventional level of statistical significance ($p = 0.062$). Notably, and in spite the fact that we
16 explored this interaction via liberal – and unprotected – paired-samples t-tests, results indicated
17 that loVF and upVF trials did not differ at matched feedback group and stereo-cue conditions.
18 Accordingly, our results provide no evidence of a loVF advantage for the planning or online
19 control of reaches to a depth target.³

20 In reconciling our work with previous studies, Khan and Lawrence (2005) required
21 reaches to be completed in a movement time criterion of $400 \pm 10\% \text{ ms}^4$ – a range permitting
22 sufficient time for online corrections (Elliott et al., 2001). In turn, average MTs in the current
23 investigation were longer (644 ms, $SD=114$) and it is therefore unlikely that information

1 processing demands – and required online corrections – account for the between-experiment
2 discrepancy. As well, both the present study and Khan and Lawrence presented targets 16°
3 above and below the central visual axis, and as a result the between-experiment difference
4 cannot relate to the eccentricity targets were presented in the vertical retinal axis. It is, however,
5 important to recognize that Khan and Lawrence employed upVF and loVF trials in separate
6 blocks. This is a salient consideration because a blocked presentation may have afforded
7 participants the opportunity to learn from previous trials (i.e., a strategic adaption and/or offline
8 learning) and may therefore not provide direct evidence of a loVF advantage for online
9 corrections (Khan, Elliott, Coull, Chua, & Lyons, 2002; Wolpert, Ghahramani, & Jordan, 1995).
10 In the present investigation, loVF and upVF reaches were randomly interleaved to ensure that the
11 depth and location of a target on participants' retina was varied on each trial – a manipulation
12 that required trial-specific sensorimotor transformations (Flanders, Helms Tillery, & Soechting,
13 1992). Concerning the between-experiment difference between our study and Danckert and
14 Goodale (2001), the latter study employed a range of IDs (0.3-1.5 bits) requiring a ballistic and
15 offline mode of control (Gan & Hoffmann, 1988). In contrast, the target ID used here (middle
16 target = 6.6 bits) is known to elicit reliable speed-accuracy relations and require online trajectory
17 amendments. Accordingly, the present results demonstrate that the anatomical asymmetry in the
18 vertical visual field coupled with the reported preferential mapping of loVF inputs to the dorsal
19 visual pathway does not infer an advantage for the online control of reaches.

20 Binsted and Heath (2005) and Krigolson and Heath (2006) reported a null loVF
21 advantage for online control; however, in those studies it was also reported that the loVF
22 produced less variable endpoints than their upVF counterparts – a finding attributed to enhanced
23 central planning in the loVF. Again, it should be noted that the just-mentioned studies used

1 computer-generated targets or targets embedded in a stimulus board, whereas the targets used
2 here were disparate in depth from the stimulus board and resulted in an equivalent tolerance for
3 loVF and upVF reaches. Accordingly, we believe that the present results add importantly to the
4 literature insomuch as they demonstrate that a vertical field asymmetry in retinal cell density,
5 and/or the reported preferred mapping of the loVF to dorsal visuomotor networks, does not
6 consistently or reliably impart a functional advantage for the planning or online control of
7 reaches.

8 One final issue requires addressing. As noted previously, Curcio and Allen's (1990)
9 work reporting that the superior retina has a 65% increase in the density of retinal ganglion cells
10 at 4 mm beyond the vertical meridian (compared to the inferior retina) is taken as direct
11 anatomical evidence for the loVF advantage for reaching. It is, however, equally necessary to
12 recognize that Curcio and Allen documented considerable variability in the retinal samples used
13 in their study (i.e., 6 human retinas including two fellow eyes) and reported that the asymmetry
14 diminished (or was absent) when disparities in the surface area of the superior and inferior retina
15 were equated. Moreover, visual processing areas including the early visual cortex (Liu, Heeger,
16 & Carrasco, 2006; Portin & Hari, 1999; Portin, Vanni, Virsu, & Harri, 1999) and the lateral
17 occipital cortex (Sayres & Grill-Spector, 2008; Strother, Aldcroft, Lavell, & Villis, 2010) have
18 shown a loVF advantage in object detection and discrimination – tasks and cortical structures
19 that are not linked to visuomotor control.

20 *Conclusions*

21 Binocular CL reaches were more efficient and demonstrated more online corrections than their
22 monocular and OL counterparts. Notably, however, increasing the reliance on the 'fast'
23 visuomotor networks of the dorsal stream did not differentially influence loVF and upVF

- 1 reaches. Accordingly, we propose that the loVF and upVF exhibit a comparable degree and
- 2 effectiveness of online corrections.

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- 23

1 Footnotes

2 1. As indicated below, four participants from the CL group and one from the OL group were
3 removed due to equipment error and signal loss. Thus, the degrees of freedom reported
4 here and the reported means for the TNO test represent the adjusted number of
5 participants in each group.

6 Because we accepted only those trials involving a ‘hit’ we did not include constant error
7 in our main Results. In support of that approach, loVF CE_X (-2.3 mm, $CI_{95\%}=4.1$), CE_Y
8 (20.5 mm, $CI_{95\%}=2.5$) and CE_Z (10.1 mm, $CI_{95\%}=2.5$) values did not reliably differ from
9 their upVF counterparts (i.e., $CE_X=-2.7$ mm, $CI_{95\%}=1.6$, $CE_Y=22.7$ mm, $CI_{95\%}=4.4$, and
10 $CE_Z=15.0$ mm, $CI_{95\%}=3.1$).

11 The present work employed 24 participants and is a sample larger than the 8, 13, 12 and
12 10 participants used respectively by Dankert and Goodale (2001), Binsted and Heath
13 (2005), Khan and Lawrence (2005) and Rossit et al. (2013). It is therefore unlikely that
14 the absence of a reliable loVF advantage is related to an inadequate replication sample
15 size (Keppel 1991). Moreover, because of the spatial correlations used here we employed
16 more trials per target ($N=50$) than previous work (i.e., $N \leq 8$) and thus provide mean
17 values that more strongly relate to the central limit theorem.

18 4. Khan and Lawrence (2005) did not report movement ID.

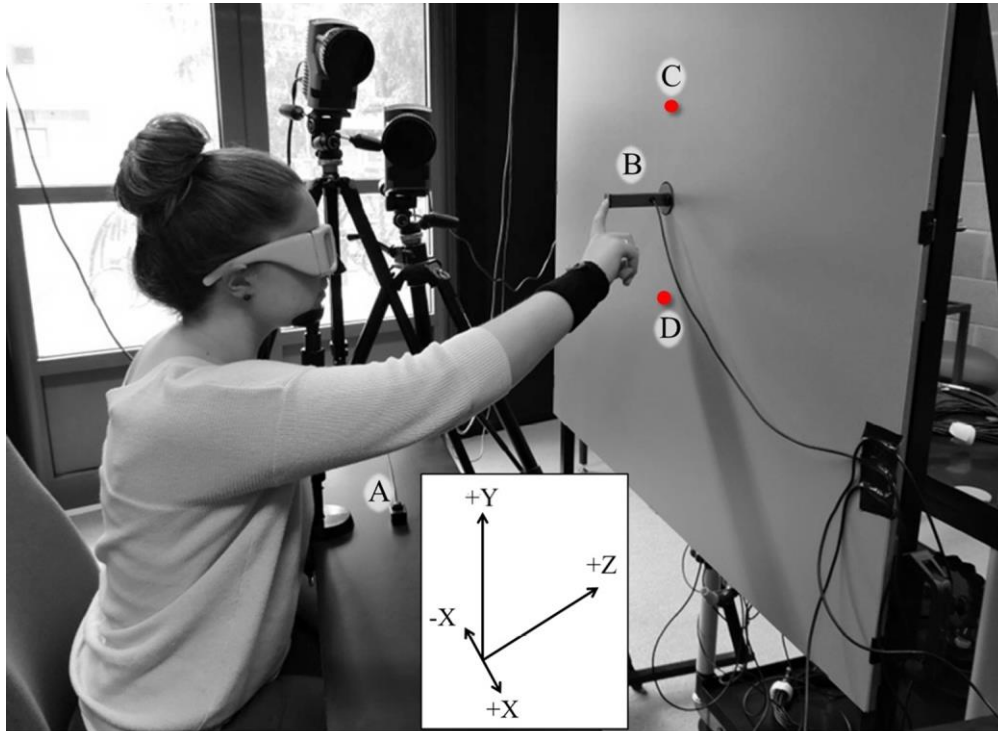
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1 **Figure Captions**

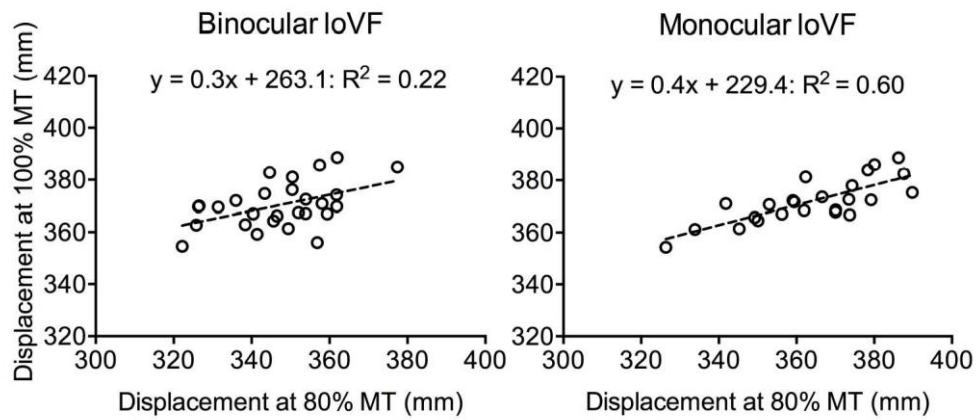
- 2 1. Picture of the experimental set-up from the experimenter's point of view. Participants began
3 each trial by pressing the home button (A) with their right index finger. To manipulate the
4 visual field in which the target (B) was presented, fixation LEDs were located above and
5 below the target. The fixation LED located above the target (C) resulted in a loVF trial,
6 whereas the fixation LED located below the target (D) resulted in an upVF trial. Note: the
7 current image demonstrates the target that was 192 mm in depth from the stimulus board (i.e.,
8 the middle target) and was the target position associated with the data analyses presented here.
9 A trial concluded once the participant had quickly and accurately reached forward and placed
10 their right index finger on the center of the target LED.
- 11 2. An exemplar participant's data showing the proportion of variance (R^2) in movement
12 endpoints (depth or Z-axis) explained by the spatial position of their limb at 80% of
13 movement time for binocular (left panel) and monocular (right panel) loVF reaches.
- 14 3. Mean movement time (MT: top panel) and percentage of time after peak velocity (%TAPV:
15 bottom panel) as a function of visual field (loVF and upVF) and stereo-cue (binocular and
16 monocular) conditions in closed-loop (CL) and open-loop (OL) groups. Error bars represent
17 95% within-participant standard deviations.
- 18 4. Variable error in each cardinal axis as a function of visual field (loVF and upVF) and stereo-
19 cue (binocular and monocular) for closed-loop (CL) and open-loop (OL) groups. Error bars
20 represent 95% within-participant standard deviations.
- 21 5. The left and right panels show mean proportion of explain variance (R^2 values) in the closed-
22 loop (CL) and open-loop (OL) groups, respectively. Each panel shows mean values at 20%,
23 40%, 60% and 80% of movement time as a function of each visual field (loVF and upVF) and

- 1 stereo-cue (binocular and monocular) condition. The top, middle and bottom panels depict R^2
- 2 values for the directional (X), distance (Y), and depth (Z) axes, respectively. Error bars
- 3 represent 95% within participant confidence intervals.



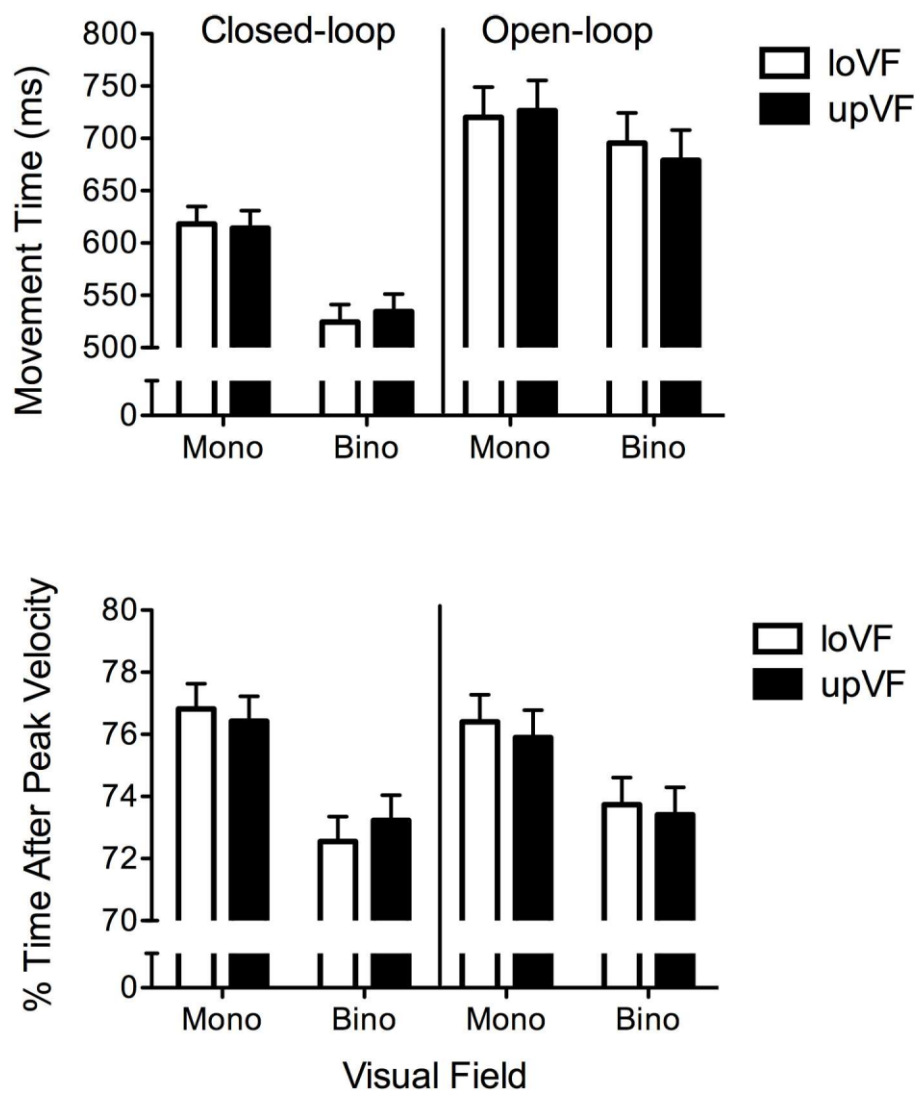
Picture of the experimental set-up from the experimenter's point of view. Participants began each trial by pressing the home button (A) with their right index finger. To manipulate the visual field in which the target (B) was presented, fixation LEDs were located above and below the target. The fixation LED located above the target (C) resulted in a loVF trial, whereas the fixation LED located below the target (D) resulted in an upVF trial. Note: the current image demonstrates the target that was 192 mm in depth from the stimulus board (i.e., the middle target) and was the target position associated with the data analyses presented here. A trial concluded once the participant had quickly and accurately reached forward and placed their right index finger on the center of the target LED.

206x152mm (150 x 150 DPI)

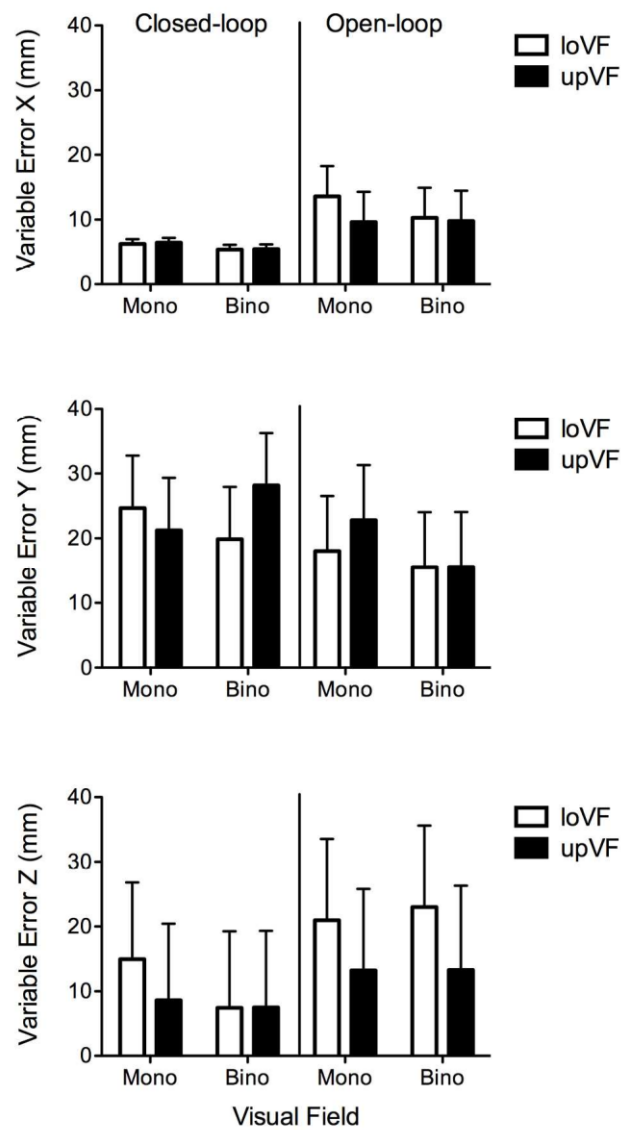


An exemplar participant's data showing the proportion of variance (R^2) in movement endpoints (depth or z-axis) explained by the spatial position of their limb at 80% of movement time for binocular (left panel) and monocular (right panel) loVF reaches.

200x90mm (300 x 300 DPI)

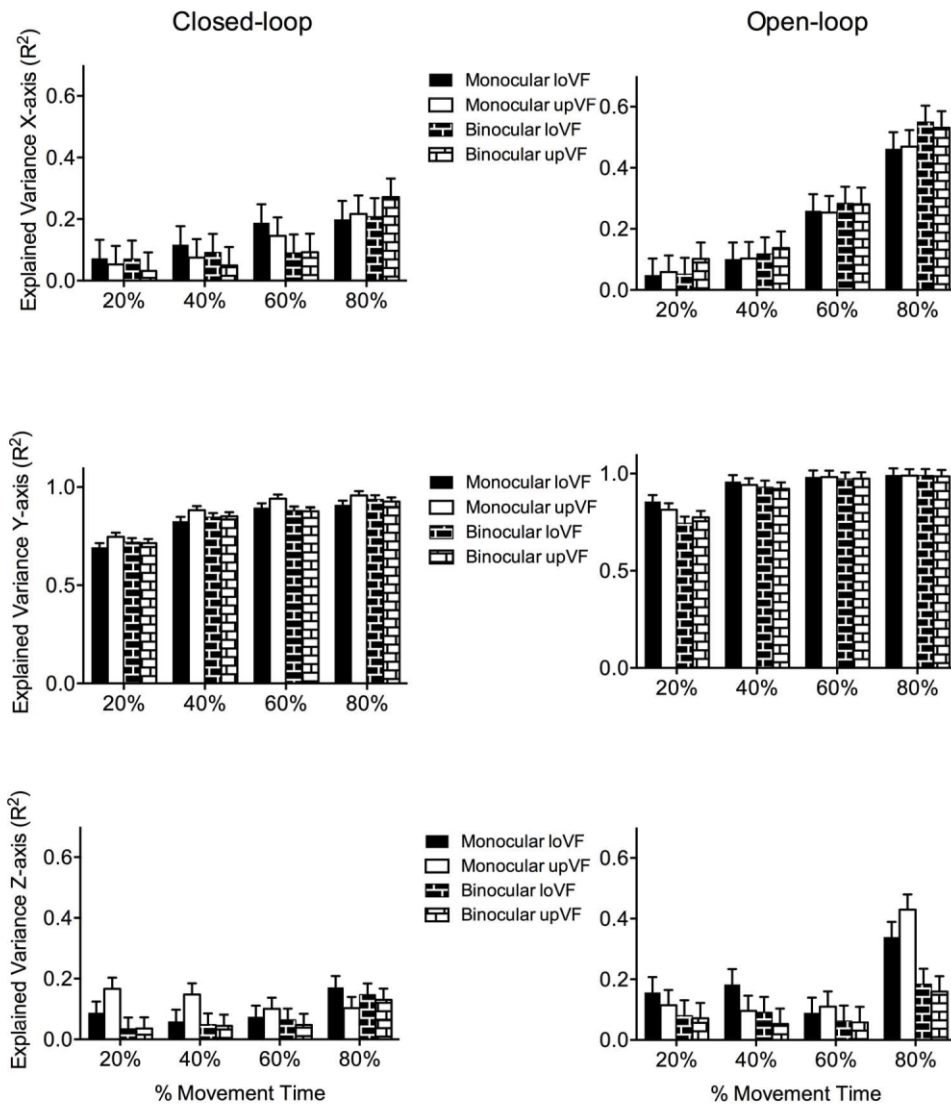


Mean movement time (MT: top panel) and percentage of time after peak velocity (%TAPV: bottom panel) as a function of visual field (loVF and upVF) and stereo-cue (binocular and monocular) conditions in closed-loop (CL) and open-loop (OL) groups. Error bars represent 95% within-participant standard deviations.



Variable error in each cardinal axis as a function of visual field (loVF and upVF) and stereo-cue (binocular and monocular) for closed-loop (CL) and open-loop (OL) groups. Error bars represent 95% within-participant standard deviations.

125x220mm (300 x 300 DPI)



The left and right panels show mean proportion of explain variance (R^2 values) in the closed-loop (CL) and open-loop (OL) groups, respectively. Each panel shows mean values at 20%, 40%, 60% and 80% of movement time as a function of each visual field (loVF and upVF) and stereo-cue (binocular and monocular) condition. The top, middle and bottom panels depict R^2 values for the directional (X), distance (Y), and depth (Z) axes, respectively. Error bars represent 95% within participant confidence intervals.

162x183mm (300 x 300 DPI)