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Ipsilateral eye contributions to online visuomotor control of right upper-limb movements

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ABSTRACT

A limb's initial position is often biased to the right of the midline during activities of daily living. Given this specific initial limb position, visual cues of the limb become first available to the ipsilateral eye relative to the contralateral eye. The current study investigated online control of the dominant limb as a function of having visual cues available to the ipsilateral or contralateral eye, in relation to the initial start position of the limb. Participants began each trial with their right limb on a home position to the left or right of the midline. After movement onset, a brief visual sample was provided to the ipsilateral or contralateral eye. On one third of the trials, an imperceptible 3 cm target jump was introduced. If visual information from the eye ipsilateral to the limb is preferentially used to control ongoing movements of the dominant limb, corrections for the target jump should be observed when movements began from the right of the body's midline and vision was available to the ipsilateral eye. As expected, limb trajectory corrections for the target jump were only observed when participants started from the right home position and visual information was provided to the ipsilateral eye. We purport that such visuomotor asymmetry specialization emerges via neurophysiological developments, which may arise from naturalistic and probabilistic limb trajectory asymmetries.

1. Introduction

The functional specialization between the dominant and non-dominant limb is referred to as manual asymmetry (e.g., Flowers, 1975; see Bryden, 2016 for a review). Previous work has extensively focused on the contribution of the dominant and non-dominant limb for activities such as reaching (e.g., Apker, Dyson, Frantz, & Buneo, 2015; Gooderham & Bryden, 2014; Sainburg & Kalakanis, 2000), grasping (e.g., Gonzalez, Whitwell, Morrissey, Ganel, & Goodale, 2007; Grosskopf & Kuhtz-Buschbeck, 2006; Le, Vesia, Yan, Niemeier, & Crawford, 2014), and throwing (e.g., van den Tillaar & Ettema, 2009). Empirical models of these goal-directed actions suggest that visual cues gathered during movement execution contribute to successful movement execution (see Elliott et al., 2017 for a recent review). Visual cues of the moving limb are gathered by both eyes; one being ipsilateral to the moving limb, and the other contralateral to the moving limb. To date, the specific contribution of visual cues gathered by the ipsilateral and contralateral eye for online control of upper limb movements have not been clearly elucidated. Thus, the current study examined the influence of early visual cues gathered during movement execution by the ipsilateral and contralateral eye.

The availability of visual feedback is integral for the successful completion of upper-limb movements (Keele & Posner, 1968;

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Woodworth, 1899; Zelaznik, Hawkins, & Kisselburgh, 1983). Indeed, when visual feedback is available during action, participants have exhibited greater accuracy and precision (e.g., Carson, Chua, Elliott, & Goodman, 1990; Carson, Goodman, Chua, & Elliott, 1993; Kennedy, Bhattacharjee, Hansen, Reid, & Tremblay, 2015; Tremblay et al., 2017) and had longer limb deceleration times (i.e., time after peak limb velocity, see: Chua & Elliott, 1993). However, processing such visual cues requires a minimum of 100 ms in order to be effective in controlling the moving limb (e.g., Carlton, 1981, 1992; Zelaznik et al., 1983). As a result, more recent work has examined the contribution of visual cues gathered early on in the trajectory to enhance terminal accuracy and precision.

Saunders and Knill (2005) introduced a directional bias by manipulating the perceived location of the fingertip (i.e., represented by a cursor on screen) at 25% and 50% of the overall movement. For perturbations introduced at 25% of the trajectory, amendments were typically observed between peak velocity and peak deceleration (i.e., online control phase of the movement). Such findings yielded further inquiry into the utility of early visual cues (i.e., visual cues typically gathered prior to peak limb velocity occurrence) relative to late visual cues (i.e., visual cues typically gathered after peak limb velocity occurrence). Kennedy et al. (2015) provided participants with visual feedback throughout the trajectory or when the real-time limb velocity was above 0.8 m/s in three different windows: early (i.e., between 0.8 and 1.4 m/s, before peak velocity), middle (i.e., above 1.4 m/s, including peak velocity), and late (i.e., between 1.4 and 0.8 m/s, after peak velocity). The results showed that movement endpoints were significantly more consistent (i.e., a measure reflecting online control) in the early and middle vision conditions than in the late and no-vision conditions. Critically, the early and middle conditions did not significantly differ from the full vision condition, suggesting that having relatively early visual cues of the trajectory may elicit online visuomotor control processes that typically occur during binocular viewing of the entire trajectory (see also Proteau, Roujoula, & Messier, 2009). However, as discussed above, visual cues can be gathered by both the ipsilateral and the contralateral eye (e.g., Porac & Coren, 1976). How are visual cues gathered by each eye then utilized for online visuomotor control?

To determine the contribution of the contralateral and ipsilateral eye for controlling an ongoing upper-limb movement, Manzone, Loria, and Tremblay (2018) had participants perform a reaching movement with the dominant right limb. All participants had an ipsilateral hand and eye dominance relationship (i.e., all right hand and right eye dominant). Indeed, about 90% of the population is right handed and of the right handed individuals, about two thirds are right eye dominant (i.e., Bourassa, McManus, & Bryden, 1996). Thus, these participants represent a majority of the population. Vision of the entire environment (i.e., the moving hand and the target) was manipulated such that participants received 20 ms of visual feedback early during the movement to either the contralateral eye (i.e., the left, non-dominant eye), the ipsilateral eye (i.e., the right, dominant eye), or to both eyes (i.e., binocular vision; see Experiment 2). A target located 30 cm away from the home position was extinguished upon movement onset and replaced by a target 27 cm away from the home position (i.e., target jump), without the participant's knowledge (e.g., Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986). The results showed that on target jump trials, movement endpoints significantly shifted towards the new target position only when visual feedback was gathered by the ipsilateral eye (i.e., monocular dominant and binocular vision conditions). Such a finding suggests that information from the ipsilateral eye is particularly important to control an ongoing limb movement. However, why would one eye (i.e., the ipsilateral eye) be specialized to control dominant limb movements? Further, one limitation of the Manzone et al. (2018) paradigm was that movements always began from a home position aligned to the body's midline. Utilizing more naturalistic starting positions of the limb may elucidate further the contributions of early ipsilateral and contralateral visual cues for online visuomotor control.

Let us consider a right handed and right eye dominant (i.e. ipsilateral eye) individual engaging in a reaching action. As shown in Fig. 1, a common upper-limb reaching movement typically begins with the dominant limb positioned alongside the individual's body (see Fig. 1, *Panel* A). Although stimuli and the majority of *peri*-personal space are well within the binocular field of view, the absolute earliest visual cues of the moving limb are available exclusively to the ipsilateral eye to the moving limb (see Fig. 1, *Panel* B) before entering the binocular crescent (Fig. 1, *Panel* C). Based on empirical/ probabilistic theories of vision (e.g., Purves & Lotto, 2003), it is possible that the visual system preferentially develops the capacity to control ongoing arm movements via the eye that is ipsilateral to the dominant hand. Indeed, the earliest visual cues (i.e., picked up by the nasal portion of the ipsilateral eye when the limb begins from a location to the right of the midline) project to the contralateral left hemisphere which, in turn, controls the dominant right limb (Fig. 1).

The current study investigated how early visual cues gathered by the ipsilateral and contralateral eye while the limb moved in left or right space (i.e., relative to the body's midline) were utilized for online control. Participants performed reaching movements from home positions displaced to the left or right of the midline towards a target that could shift imperceptibly after movement onset. Importantly, the finger at both home positions was visible to both the ipsilateral and contralateral eyes, and thus, it is likely that both eyes had access to the same visual cues, prior to movement onset. However, the displacement in initial start position was expected to influence visuomotor control online (i.e., when the window of vision was provided), in relation to which eye gathered visual cues of the movement trajectory. Specifically, larger corrections for targets shifts (i.e., shorter movement amplitudes) were expected when visual information was available to the eye that was ipsilateral to the moving limb relative to the contralateral eye (i.e., Manzone et al., 2018). Also, presuming that the ipsilateral eye is specialized to process feedback of the limb within the ipsilateral binocular hemispace (see Fig. 1), movements were expected to be more accurate when vision was available to the ipsilateral eye overall when reaching began from the right home position.
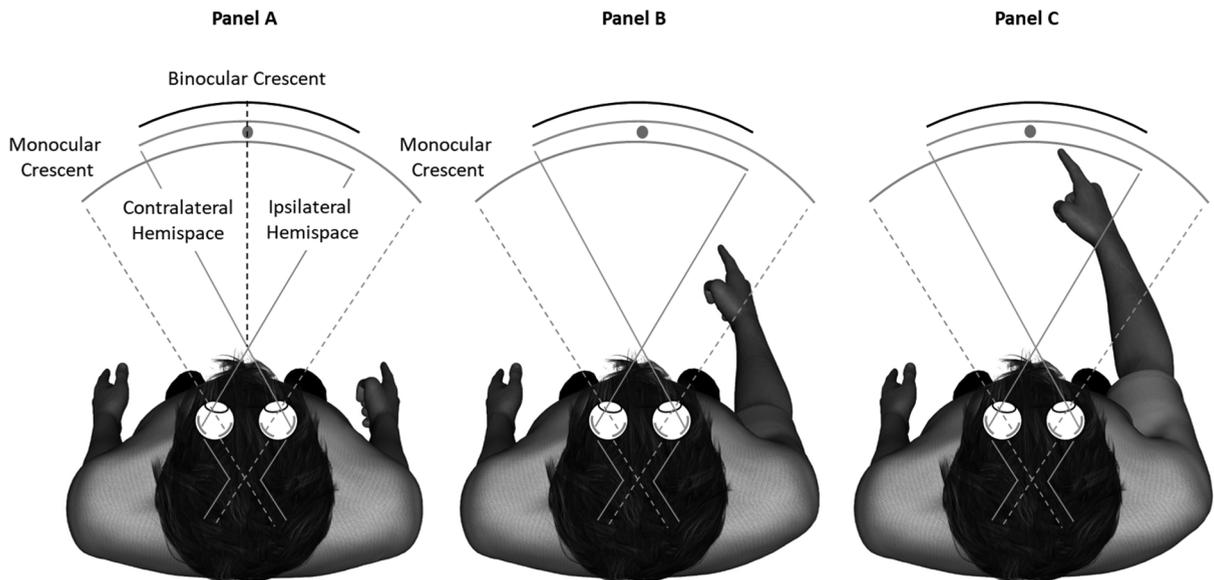
Fig. 1. Depiction of a right eye and right hand dominant individual performing a sample reaching movement into their ipsilateral hemispace with their dominant limb. The limb is initially out of sight prior to movement onset (Panel A). At early stages of the movement, visual information is available in the monocular crescent of the dominant right eye (Panel B) before entering the binocular crescent toward movement end (Panel C). Visual information that strikes the nasal portion of the eyes is depicted with dotted lines and projects to the contralateral hemifield in the brain. Visual information that strikes the temporal portion of the eyes is depicted with solid lines and projects to the ipsilateral hemifield in the brain.

2. Methods

2.1. Participants

Thirteen members of the University of Toronto community (8 females, M = 23 years, SD = 4.1 years) provided written informed consent prior to participation. Right-hand dominance was confirmed via the Edinburgh Inventory (i.e., Oldfield, 1971). Further, eye dominance was assessed with an eye-target alignment test (i.e., Miles, 1930). In addition, participants were asked what eye they would use to complete a monocular task (i.e., "looking through a keyhole" and "looking through a camera view finder"). All participants exhibited an eye-target alignment with their right eye and reported using their right eye for both monocular tasks. The experimental session lasted approximately thirty minutes, and participants were compensated $5 CAD.

2.2. Apparatus

Participants sat on an adjustable kneeling chair with an aiming console (width: 27.5 cm, length: 50 cm, height: 8 cm) positioned in front of a desk along the mid-sagittal axis (see Fig. 2). The surface of the aiming console was covered with a translucent polymer sheet. Participants directed their gaze to a fixation-cross located at the bottom of the aiming console, which was aligned with the participant's midline. The fixation point was flanked on either side by home positions (1 cm^2) located 12 cm to the left (i.e., left home position) and 12 cm to the right (i.e., right home position) of fixation. In order to ensure that movements occurred within the ipsilateral or contralateral binocular crescents, the home positions were shifted 1 cm above fixation (e.g., Prablanc, Echallier, Jeannerod, & Komilis, 1979). Beneath the surface of the aiming console were two green 5 mm light emitting diodes (LEDs) located 30 and 27 cm away from the fixation point. The targets could not be seen from under the polymer sheet when extinguished. Participants were cued to begin their movement via an auditory beep generated by a piezo-electric buzzer (2900 Hz: Sonalert SC416; Mallory Inc., Indianapolis, IN, USA).

Participant's vision of the environment was controlled using liquid–crystal occlusion spectacles (Translucent Technologies Inc., Toronto, ON, Canada; see Milgram, 1987), which could be transparent (i.e., glass-like) or translucent (i.e., "milky"). The goggles were used to provide vision to the contralateral (i.e., left), ipsilateral (i.e., right), or both eyes (i.e., binocular vision). An Optotrak Certus (Northern Digital Inc., Waterloo, ON, Canada) motion tracking system monitored an infra-red light emitting diode (IRED) at 500 Hz during the aiming movements. The IRED was taped to the dorsal side of the participant's right index finger. A custom MATLAB (MathWorks Inc., Natick, MA, USA) script was used to gather data from the Optotrak and control the LEDs and liquid–crystal goggles via a data acquisition board (PCI-6024e, National Instruments Inc., Austin, TX, USA). Based on MATLAB processing and hardware transmission delays, the time taken to change the state of the liquid-crystal goggles (i.e., transparent or translucent) was estimated to be less than 10 ms.
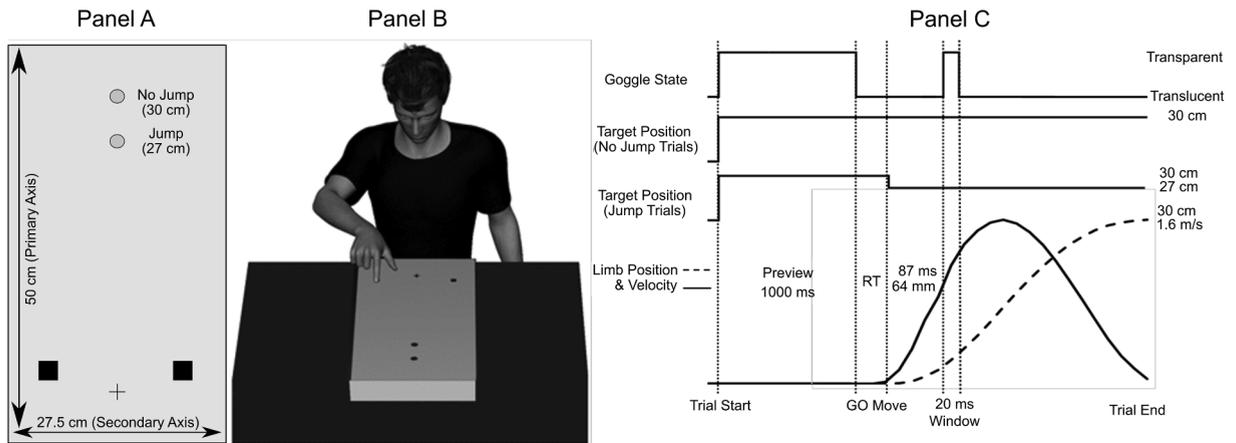
Panel A   Panel B   Panel C

Fig. 2. Depiction of the aiming console employed in the current study (Panel A) with dimensions and arrangements of home positions (black squares), start fixation position (plus sign), and targets (circles). Panel B depicts a trial starting from the right home position. Panel C depicts the trial timeline including the goggle state, the target positions, and the average displacement and velocity profile across all subjects. As depicted in the timeline, on target jump trials the target was displaced when the goggles were in a translucent state and the visual window was available, on average, 87 ms and 64 mm into the movement.

2.3. Procedure

On every trial, participants were instructed to look straight down onto the fixation point. Movements of the head were only permitted between the experimental trials and were monitored by the experimenter. Participants were provided with a 1000 ms binocular preview of the environment that included the 30 cm target, the fixation point, and the participant's limb at the left or right home position. Following the preview, the goggles became translucent (i.e., no vision) and a "go" signal was presented (i.e., the piezo-electric buzzer sounded for 20 ms). At this time, participants were instructed to perform a saccade to the target. Indeed, additional work has shown that participants saccade from the home position to the target location prior to the onset of the reaching action (i.e., de Brouwer, Albaghdadi, Flanagan, & Gallivan, 2018). As such, it was presumed that participants were fixating on the target location when reaching. During the limb's trajectory, a 20 ms window of vision was provided when the limb reached a velocity of 1.0 m/s for one sample. This specific velocity criterion was chosen because it has been associated with online limb-target regulation processes for movements performed to 30 cm targets within an approximate 325–375 ms movement time bandwidth (e.g., Tremblay et al., 2017; Tremblay, Hansen, Kennedy, & Cheng, 2013). On average, this 20 ms window of vision was provided 87 ms after movement start and 64 mm into the movement, which is relatively early in the trajectory. Although the hand would normally cross the line of sight when moving from the left home position, this early visual feedback avoided such a potential confound.

Three vision conditions were employed: contralateral vision (i.e., vision to the contralateral eye relative to the moving limb), ipsilateral vision (i.e., vision to the ipsilateral eye relative to the moving limb), and binocular (i.e., vision to both eyes). Despite the interest in contralateral and ipsilateral contributions to limb-control, the binocular condition was included, in part, to replicate the Manzone et al. (2018) findings, and to gain further insight into contralateral and ipsilateral contributions to binocular vision. In the contralateral condition, the left lens of the goggles became transparent. In the ipsilateral condition, the right lens of the goggles became transparent. In the binocular condition, both lenses became transparent. During the transparent state, visual information of the target and limb position was available to the participant. The time taken by the goggles to change state is between 2 and 4 ms (Milgram, 1987). The processing time by MATLAB and change of state of the digital output signal was approximately 2 ms, with an estimated standard deviation of less than 1 ms. Following the 20 ms window of vision, the goggles once again became translucent. Upon movement completion, the participant's finger remained at its terminal position until the piezo-electric buzzer sounded again for 20 ms prompting participants to return to the home position specified for that block of trials.

Participants were first habituated to this experimental protocol via a familiarization during which 5 aiming movements were completed to the 30 cm target under all experimental visual and home position conditions resulting in 30 familiarization trials. During the experimental trials, the target could jump following the preview of the environment. On such target jump trials, the 30 cm target was extinguished, and the 27 cm target was illuminated following movement initiation (i.e., while the goggles remained translucent). Therefore, visual information of the new target position was available to the participant only when the goggles became transparent for 20 ms. Target jumps occurred on one third of trials within each block and were presented in a pseudorandomized fashion (i.e., no more than two consecutive jump trials). Participants completed 30 trials from each home position, resulting in 60 trials per vision condition (i.e., contralateral, ipsilateral and binocular) in a blocked and counter-balanced order, for a total of 180 experimental trials. When the experimental trials were completed, participants were explicitly asked whether they detected the target jump. If participants reported seeing the target shift, they were excluded from formal data analysis (n = 2). As such, the data reported

below is from participants who did not consciously perceive the target jump.

2.4. Data analysis & hypothesis testing

The main hypothesis was that visual cues gathered by the ipsilateral eye in the right side of space would yield shorter movement endpoints on jump relative to no-jump trials. To test this hypothesis paired samples t-tests and a follow-up omnibus 3 vision condition (contralateral, ipsilateral, binocular) × 2 home position (left or right) × 2 target position (jump or no jump) repeated-measures ANOVA were conducted for mean movement endpoints values along the sagittal axis (END-S). Bonferroni corrected t-tests (i.e., corrected alpha threshold of $p < 0.017$) for jump and no jump trials were contrasted within vision conditions (i.e., contralateral, ipsilateral, and binocular) when movements began from the right home position only. Because the ability to correct the movement's endpoint was expected to be specific to conditions in which the ipsilateral eye gathered feedback, equivalence tests (i.e., two one-sample t-tests) were carried out contrasting jump and no jump movement endpoints for both home positions in the contralateral vision condition. Equivalence tests were carried out using Minitab version 18.1 (Minitab Inc., Sate College, PA, USA). The equivalence bounds were determined by referencing the amount of correction for movements with vision provided at 1.0 m/s in Manzone et al. (2018) and Tremblay et al. (2017). The resulting equivalence bound was ± 10 mm.

The vision and home position manipulations were expected to yield additional kinematic effects (i.e., reported below under Follow-up Analyses). Exploratory analyses were conducted on movement timing and kinematic related variables. Movement time (MT) was the time in milliseconds from when the limb's velocity first reached a threshold of 0.03 m/s (i.e., movement start) until the limb's velocity fell below 0.03 m/s (i.e., movement end), and time after peak limb velocity (TAPV) was the time in milliseconds from when the limb reached its highest velocity until movement end. The kinematic variables analyzed were movement amplitude at window onset, which was defined as the distance in millimeters when 1.0 m/s was reached, and the goggles became transparent. END-ML was the average movement endpoint along the medial-lateral axis. END-ML values are relative to the target position such that 0 represents the target position itself, negative values represent endpoints to the left of the target and positive values represent endpoints to the right of the target (see Table 1). The kinematic variables outlined above were submitted to exploratory 3 vision condition (contralateral, ipsilateral, binocular) × 2 home position (left or right) × 2 target position (jump or no jump) repeated-measures ANOVAs. When significance was reached, post-hoc comparisons were made using Bonferroni corrected t-tests, with appropriately adjusted α values.

3. Results

A detailed summary of the dependent variables data can be found in Table 1.

3.1. Movement endpoint hypothesis test

Contrasts of END-S for jump and no jump trials when the limb began from the right home position were carried out within the vision conditions. Significant movement endpoint corrections for the target jump only occurred when movements began from the right home position in the ipsilateral visual condition (t (12) = 3.79, p = .003, 95% CI [5.62, 20.80]) and binocular viewing

Table 1
Data for movement time (MT), time after peak limb velocity (TAPV), medial-lateral axis endpoint (END-ML) and sagittal axis endpoint (END-S) are shown as a function of target position, home position, and vision condition. The values in bold indicate that jump and no jump trials were significantly different for END-S.

| Vision condition/home position	MT (ms)		TAPV (ms)		END-ML (mm)		END-S (mm)	
	Target condition							
	No Jump M (SD)	Target Jump M (SD)	No Jump M (SD)	Target Jump M (SD)	No Jump M (SD)	Target Jump M (SD)	No Jump M (SD)	Target Jump M (SD)
Contralateral/								
Left	332.5 (56.7)	324.1 (50.6)	192.8 (35.1)	186.1 (30.3)	2.65 (25.3)	4.35 (24.5)	334.7 (37.1)	333.1 (43.3)
Right	387.6 (40.2)	382.5 (38.4)	206.1 (25.3)	198.5 (24.9)	−3.11 (27.1)	−0.93 (25.5)	337.2 (49.1)	337.4 (47.3)
Binocular/								
Left	343.7 (53.9)	323.3 (46.9)	200.9 (32.5)	182.5 (32.1)	−2.79 (24.5)	−4.77 (27.1)	326.1 (40.2)	318.1 (37.8)
Right	388.6 (45.6)	374.9 (45.1)	202.6 (26.9)	196.7 (30.7)	−5.92 (19.5)	−5.43 (20.5)	**329.4 (44.3)**	**318.3 (38.6)**
Ipsilateral/								
Left	315.5 (60.4)	306.8 (58.5)	189.2 (31.1)	178.1 (27.5)	−2.34 (27.2)	−3.73 (25.8)	321.4 (38.2)	317.4 (36.4)
Right	380.4 (51.2)	363.1 (41.3)	201.5 (30.1)	195.5 (22.9)	−7.42 (19.3)	−6.07 (18.7)	**327.1 (38.4)**	**313.8 (40.2)**
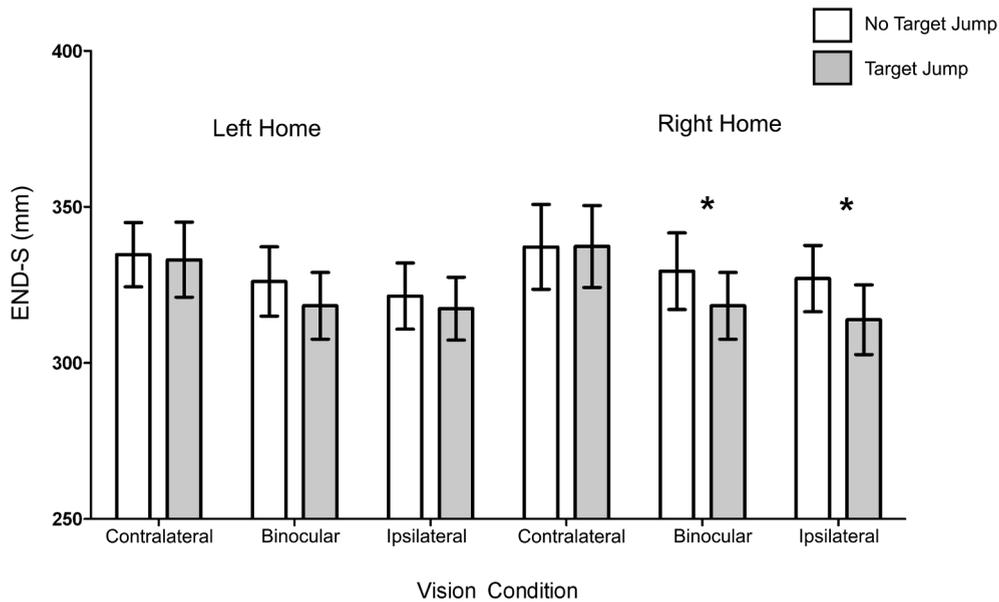
Fig. 3. Average endpoint position along the sagittal axis (i.e., primary movement axis) across all experimental conditions.

conditions (t (12) = 3.71, p = .003, 95% CI [4.58, 17.61]; all other ps > .008[1]; see Fig. 3). In addition, equivalence tests were used to determine whether movement endpoint differences were meaningful (i.e., not equivalent) within the contralateral vision condition for both home positions. The equivalence test contrasting average movement endpoints that originated from the left home position for jump and no jump trials revealed the two conditions were equivalent, t (12) = −2.9, p = 0.01 (i.e., highest p value). In addition, the same test performed for the right home position again yielded equivalence, t (12) = 3.61, p = 0.002 (i.e., highest p value). That is, meaningful amendments to movement endpoints only occurred when vision was available to the ipsilateral eye, and movements began from the right home position.

3.2. Follow-up analyses

We further examined the interplay between vision conditions, home positions, and target locations via an omnibus test. The ANOVA conducted on END-S yielded a main effect of vision condition (F (2, 24) = 5.29, p = .013, n_p^2=0.31), target position (F (1, 12) = 35.52, p < .001, n_p^2=0.78), and a significant vision by target position interaction (F (2, 24) = 3.49, p = .047, n_p^2=0.23). For the main effect of vision, Bonferroni corrected t-tests (i.e., corrected alpha threshold of p = .017 for the 3 contrasts) revealed that endpoints were significantly shorter in amplitude (i.e., endpoints that are closer to the target's position) in the ipsilateral visual condition (M = 320 mm, SD = 37.5 mm, Error = 20 mm) than the contralateral visual condition (M = 335 mm, SD = 43.2 mm, Error = 35 mm; t (12) = 2.89, p = .014, 95% CI [3.87, 27.47]). No other differences reached significance (i.e., all ps > 0.017).[2] The main effect of target position showed that movement endpoints were significantly greater when reaching towards the no jump (M = 329 mm, SD = 40.4) than the jump target positions (M = 323 mm, SD = 40.3). To decompose the vision by target interaction, Bonferroni corrected t-tests (i.e., corrected alpha threshold of p = .017) confirmed that participant's endpoints were significantly closer to the new target location (i.e., corrections) in the jump compared to the no jump trials, only in the ipsilateral (M$_{difference}$ = 9 mm, SD = 12 mm; t (12) = 2.96, p = .012, 95% CI [2.28, 14.96]) and binocular conditions (M$_{difference}$ = 10 mm, SD = 10 mm; t (12) = 4.33, p = .001, 95% CI [4.77, 14.43]; cf. contralateral condition, M$_{difference}$ = 1 mm, SD = 9.7 mm; t (12) = 0.39, p = .702, 95% CI [−3.35, 4.83]).

The analysis of the movement time yielded a main effect of home position (F (1, 12) = 65.73, p < .001, n_p^2=0.85) and target position (F (1, 12) = 14.96, p = .002, n_p^2=0.56). Movement times were significantly shorter when starting from the left (M = 324 ms, SD = 54.2) than the right (M = 380 ms, SD = 43.2) home position. Further, movement times were significantly longer for no jump (M = 358 ms, SD = 57.8) than jump (M = 346 ms, SD = 54.1) trials. No other main effects or interactions yielded significance.

Analysis of time after peak limb velocity yielded a main effect of home position (F (1, 12) = 17.42, p = .001, n_p^2=0.59) and target position (F (1, 12) = 8.21, p = .014, n_p^2=0.41). Time spent after peak limb velocity was greater when movements began from the right (M = 200 ms, SD = 26.3 ms) than the left (M = 188 ms, SD = 31.3 ms) home position. Also, more time was spent after peak

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[1] The difference in END-S in the jump and no jump trials when starting from the left home position in the binocular viewing condition approached statistical significance (t (12) = 2.62, p = .023, 95% CI [1.35, 14.86]).

[2] The difference in END-S between the binocular (322 mm) and monocular non-dominant vision condition approached statistical significance (t (12) = 2.53, p = .026, 95% CI [1.76, 23.49]).

limb velocity when reaching to the no jump (M = 199 ms, SD = 29. 9 ms) than the jump target (M = 190 ms, SD = 28.4 ms). Analysis of END-ML did not yield any main effects or significant interactions, and therefore was not further analyzed.

Analysis of movement amplitude at window onset yielded a main effect of home position ($F(1, 12) = 23.20, p < 0.001, n_p^2 = 0.66$) and a vision by target interaction ($F(2, 24) = 4.81, p = .017, n_p^2 = 0.29$). The main effect of home position indicated that the goggles became transparent at a shorter distance along the primary movement axis, when starting movements from the left (M = 54.4 mm, SD = 14.9) than the right home position (M = 75.8 mm, SD = 19.5). For the vision by target interaction, Bonferroni corrected t-tests (i.e., corrected alpha threshold of $p = .017$ for 3 contrasts) revealed that the goggles only became transparent at a shorter distance when pointing to the 27 cm target (M = 60.5 mm, SD = 15.4) compared to the 30 cm target (M = 64.6 mm, SD = 17.9) in the binocular vision ($t(12) = 3.5, p < .01$, 95% CI [1.56, 6.70]).

4. Discussion

The current study examined how visual cues gathered by the ipsilateral and contralateral eye were utilized for online limb-target visuomotor control processes. Prior to each trial, participants fixated on a central location at the midline, and placed their right hand on a home position either to the left or right of fixation. Vision was unavailable throughout the trajectory except for an early 20 ms window, provided to the ipsilateral eye to the moving limb, the contralateral eye to the moving limb, or to both eyes. On one third of the trials, the typically occurring 30 cm target was extinguished and a 27 cm target was illuminated (i.e., unknown to the participant). The primary goal of the current study was to determine whether the participants adjusted their movement endpoint towards the new target position as a function of vision condition (i.e., contralateral, ipsilateral, and binocular) and home position (i.e., left or right). The results showed that movements that began from the right home position with visual feedback available to the ipsilateral eye (i.e., ipsilateral and binocular vision conditions) elicited significant endpoint shifts while the differences did not reach significance in the contralateral vision conditions. The results were interpreted in relation to both biomechanical and motor control theory considerations and explained with regard to empirical theories and neurophysiological evidence.

4.1. Biomechanical and motor control considerations

From biomechanical and motor control perspectives, the observed results require some explanations and clarification. The asymmetries in movement times, and the movement amplitude at window onset can be explained by biomechanical constrains due to anatomical asymmetries. Indeed, rightward limb movements have been shown to be shorter relative to leftward movements (see Carey, Hargreaves, & Goodale, 1996; Carey & Otto-de Haart, 2001; Fisk & Goodale, 1985). Carey and Otto-de Haart (2001) explained that rightward and leftward limb movements can invoke different amounts of inertia due to the forearm and arm anatomy (see also Gordon, Ghilardi, Cooper, & Ghez, 1994). The leftward-forward reaches involve significant flexion at the shoulder and extension at the elbow, whereas rightward-forward reaches can benefit from the smaller inertia required for the rotations at the shoulder joint. In the current study, movements that began from the left home position to rightward targets yielded shorter movement times than when starting from the right home position to leftward targets. These observed differences in movement time reflect, at least in part, biomechanical differences in limb movement asymmetries (i.e., Carey & Otto-de Haart, 2001). In turn, due to the larger inertia for leftward than rightward movements, one would expect that correcting for target shifts would require more energy and time when reaching leftward than rightward. However, the pattern of results was opposite.

Regarding the utilization of visual feedback, movement endpoints were shorter in amplitude when feedback was available to the ipsilateral eye, only when the hand started from the right home position (i.e., space and eye were congruent). This finding corroborates those reported by Manzone et al. (2018) and can be incorporated into current models of online control, specifically the Multiple Process Model of Goal-Directed Reaching (i.e., Elliott et al., 2010, 2017). The current results help extend the model to include the contribution of visual cues gathered by the ipsilateral eye within ipsilateral space for limb-target regulation processes (i.e., the target jump conditions). Specifically, recent evidence suggests that the provision of visual feedback when the limb travels in the vicinity of 1.0 m/s is optimal to engage in limb-target regulation processes (e.g., Manzone et al., 2018; Tremblay et al., 2013, 2017). Typically, the CNS compares online feedback of the movement (from vision and/or proprioception) to information of the target position in order to make any necessary amendments to the ongoing trajectory. In the current study, visual cues of the participant's limb projected onto the parafoveal region of the eye when visual information was available (i.e., at 1.0 m/s, the limb was on average 64 mm into the movement). As such, it can be postulated that parafoveal cues my play a key role when initiating online movement corrections in general, a statement that is consistent with empirical and neurophysiological considerations.

One challenge the perceptual system must overcome is decoding the ambiguous visual environment (e.g., a baseball batter tracking the speed of a fast ball, or an individual determining the boundaries of an object under low luminance). Visual information is ultimately then used to plan and execute goal-directed actions (i.e., Elliott et al., 2010, 2017; Purves, Lotto, Williams, Nundy, & Yang, 2001). In the current study, the most naturalistic reaching condition was when eye and space were congruent (i.e., ipsilateral eye and right home position) relative to the incongruent eye and space combinations (i.e., contralateral eye and left home position). Perhaps, the effect of congruency is driven by a relative lack of ambiguity of both visual and motor cues, thus yielding corrections for the target jump.

However, it is important to consider that the contralateral eye had access to the same visual cues as the ipsilateral eye. Yet, the results showed an advantage for using visual information from the ipsilateral eye. As discussed in the Introduction, the earliest information pertaining to the limb's trajectory are gathered by the ipsilateral eye within the monocular crescent (see Fig. 1). Because

of this congruent coupling, it is theoretically plausible that a dedicated neuro-circuit between the ipsilateral eye and limb would develop over time (i.e., Hebbian theory). Such a persistent coupling may yield adaptations in the neurons serving the ipsilateral eye and limb to work more efficiently together. A hypothesis such as this is further supported by the quantitative increase in myelination between frequently co-activated neurons (e.g., Gibson et al., 2014), and the reverse instance in which nerve conduction velocity of the optic nerve was reduced in the absence of visual stimulation in mice (i.e., Etxeberria et al., 2016). Taken together, both theoretical and neurophysiological accounts support the observed congruent eye and hand advantage observed here.

Last but not least, it is important to emphasize is that the current study solely investigated right-hand dominant individuals using their right hand. The above-mentioned theoretical explanations require further empirical testing, which could include at least two lines of investigation. First, it would be relevant to empirically test whether there is a left eye advantage in left-hand dominant individuals reaching with their left hand. However, such investigations may be challenging considering the greater neurophysiological heterogeneity in the left-hand dominant population (see Ocklenburg & Güntürnkün, 2017). As such a second line of research could also include testing whether right-handed individuals would exhibit greater capacity to implement online trajectory amendments with their dominant vs. their non-dominant hand.[3]

5. Conclusion

The current study provided original evidence that visual cues associated with ipsilateral space and eye combinations are utilized more effectively to control a moving limb than contralateral eye and space combinations. Such results extend the knowledge of the importance of monocular contributions to limb-control. Future research should expand this work to left-hand and left-eye dominant individuals, as well as those with incongruent hand and eye dominance patterns. Conducting this line of research will likely further uncover how visual cues are utilized to control human movement.

Declaration of Competing Interest

The authors have no financial interest or benefit that may arise from the direct application of this research.

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References

Apker, G. A., Dyson, K., Frantz, G., & Buneo, C. A. (2015). Efficiency of visual feedback integration differs between dominant and non-dominant arms during a reaching task. *Experimental Brain Research, 233*, 316–327. https://doi.org/10.1007/s00221-014-4116-5.

Bourassa, D. C., McManus, I. C., & Bryden, M. P. (1996). Handedness and eye-dominance: A meta-analysis of their relationship. *Laterality, 1*(1), 5–34. https://doi.org/10.1080/713754206.

Bryden, P. J. (2016). The influence of M. P. Bryden's work on lateralization of motor skill: Is the preferred hand selected for and better at tasks requiring a high degree of skill? *Laterality: Asymmetries of Body, Brain and Cognition, 21*(4–6), 312–328. https://doi.org/10.1080/1357650X.2015.1099661.

Carey, D. P., Hargreaves, E. L., & Goodale, M. A. (1996). Reaching to ipsilateral or contralateral targets: Within-hemisphere visuomotor processing cannot explain hemispatial differences in motor control. *Experimental Brain Research, 112*(3), 496–504. https://doi.org/10.1007/BF00227955.

Carey, D. P., & Otto-de Haart, E. G. (2001). Hemispatial differences in visually guided aiming are neither hemispatial nor visual. *Neuropsychologia, 39*(9), 885–894. https://doi.org/10.1016/S0028-3932(01)00036-7.

Carlton, L. G. (1981). Processing visual feedback information for movement control. *Journal of Experimental Psychology: Human Perception and Performance, 7*(5), 1019. https://doi.org/10.1037/0096-1523.7.5.1019.

Carlton, L. G. (1992). Visual processing time and the control of movement. *Advances in psychology* (pp. 3–31). . https://doi.org/10.1016/S0166-4115(08)62011-7.

Carson, R. G., Chua, R., Elliott, D., & Goodman, D. (1990). The contribution of vision to asymmetries in manual aiming. *Neuropsychologia, 28*(11), 1215–1220. https://doi.org/10.1016/0028-3932(90)90056-T.

Carson, R. G., Goodman, D., Chua, R., & Elliott, D. (1993). Asymmetries in the regulation of visually guided aiming. *Journal of Motor Behavior, 25*(1), 21–32. https://doi.org/10.1080/00222895.1993.9941636.

Chua, R., & Elliott, D. (1993). Visual regulation of manual aiming. *Human Movement Science, 12*(4), 365–401. https://doi.org/10.1016/0167-9457(93)90026-L.

de Brouwer, A. J., Albaghdadi, M., Flanagan, J. R., & Gallivan, J. P. (2018). Using gaze behavior to parcellate the explicit and implicit contributions to visuomotor learning. *Journal of Neurophysiology, 120*(4), 1602–1615. https://doi.org/10.1152/jn.00113.2018.

Elliott, D., Hansen, S., Lyons, J., Grierson, L. E. M., Bennett, S. J., & Hayes, S. J. (2010). Goal-Directed aiming: Two components but multiple processes. *Psychonomic Bulletin and Review, 136*(6), 1023–1044. https://doi.org/10.1037/a0020958.

Elliott, D., Lyons, J., Hayes, S. J., Burkitt, J. J., Roberts, J. W., Grierson, L. E. M., ... Bennett, S. J. (2017). The multiple process model of goal-directed reaching revisited. *Neuroscience and Biobehavioral Reviews, 72*, 95–110. https://doi.org/10.1016/j.neubiorev.2016.11.016.

Etxeberria, A., Hokanson, K. C., Dao, D. Q., Mayoral, S. R., Mei, F., Redmond, S. A., ... Chan, J. R. (2016). Dynamic modulation of myelination in response to visual stimuli alters optic nerve conduction velocity. *Journal of Neuroscience, 36*(26), 6937–6948. https://doi.org/10.1523/JNEUROSCI.0908-16.2016.

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[3] In a pilot study, right-handed participants completed the same experimental paradigm as in the current study, while aiming with either their right or left limb. Participants exhibited comparable magnitudes of corrections to those reported in the current study, specifically in the ipsilateral and binocular vision conditions, and right home position. However, this was only the case the right hand trials were performed first. In contrast, participants who first completed the left-hand block of trials yielded smaller correction magnitudes with both the left and right hand. Overall, although these findings should be interpreted with caution due to the possible hand-based ordering effects, the preliminary results for the right-hand reaching movements lend additional support to our ipsilateral eye and hand facilitation interpretation.

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral visual space. *Experimental Brain Research, 60*(1), 159–178. https://doi.org/10.1007/BF00237028.

Flowers, K. (1975). Handedness and controlled movement. *British Journal of Psychology, 66,* 39–52. https://doi.org/10.1111/j.2044-8295.1975.tb01438.x.

Gibson, M. E., Purger, D., Mount, C. W., Goldstein, A. K., Lin, G. L., Wood, L. S., ... Monje, M. (2014). Neuronal activity promotes oligodendrogenesis and adaptive myelination in the mammalian brain. *Science, 344*(6183), 480–481. https://doi.org/10.1126/science.1254446.

Gonzalez, C. L. R., Whitwell, R. L., Morrissey, B., Ganel, T., & Goodale, M. A. (2007). Left handedness does not extend to visually guided precision grasping. *Experimental Brain Research, 182*(2), 275–279. https://doi.org/10.1007/s00221-007-1090-1.

Goodale, M. A., Pélisson, C., & Prablanc, C. (1986). Large adjustments in visually guided reaching do not depend on vision of the hand or perception of target displacement. *Nature, 320,* 748–750. https://doi.org/10.1038/320748a0.

Gooderham, S. E., & Bryden, P. J. (2014). Does your dominant hand become less dominant with time? The effects of aging and task complexity on hand selection. *Developmental Psychobiology, 56*(3), 537–546. https://doi.org/10.1002/dev.21123.

Gordon, J., Ghilardi, M. F., Cooper, S. E., & Ghez, C. (1994). Accuracy of planar reaching movements - II. Systematic extent errors resulting from inertial anisotropy. *Experimental Brain Research, 99*(1), 112–130. https://doi.org/10.1007/BF00241416.

Grosskopf, A., & Kuhtz-Buschbeck, J. P. (2006). Grasping with the left and right hand: A kinematic study. *Experimental Brain Research, 168*(1–2), 230–240. https://doi.org/10.1007/s00221-005-0083-1.

Keele, S. W., & Posner, M. I. (1968). Processing of visual feedback in rapid movements. *Journal of Experimental Psychology, 77*(1), 155–158. https://doi.org/10.1037/h0025754.

Kennedy, A., Bhattacharjee, A., Hansen, S., Reid, C., & Tremblay, L. (2015). Online vision as a function of real-time limb velocity: Another case for optimal windows. *Journal of Motor Behavior, 47*(6), 465–475. https://doi.org/10.1080/00222895.2015.1012579.

Le, A., Vesia, M., Yan, X., Niemeier, M., & Crawford, J. D. (2014). The right anterior intraparietal sulcus is critical for bimanual grasping: A TMS study. *Cerebral Cortex, 24*(10), 2591–2603. https://doi.org/10.1093/cercor/bht115.

Manzone, D., Loria, T., & Tremblay, L. (2018). I spy with my dominant eye. *Journal of Motor Behavior, 50*(3), 330–342. https://doi.org/10.1080/00222895.2017.1363693.

Miles, W. R. (1930). Ocular dominance in human adults. *Journal of General Psychology, 3*(3), 412–430. https://doi.org/10.1080/00221309.1930.9918218.

Milgram, P. (1987). A spectacle-mounted liquid-crystal tachistoscope. *Behavior Research Methods, Instruments, & Computers, 19*(5), 449–456. https://doi.org/10.3758/BF03205613.

Ocklenburg, S., & Güntürnkün, O. (2017). *The lateralized brain: The neuroscience and evolution of hemispheric asymmetries.* London: Academic Press.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9,* 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.

Pélisson, D., Prablanc, C., Goodale, M. A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb - II. Evidence of fast unconscious processes correcting the trajectory of the hand to the final position of a double-step stimulus. *Experimental Brain Research, 62*(2), 303–311. https://doi.org/10.1007/BF00238849.

Porac, C., & Coren, S. (1976). The dominant eye. *Psychological Bulletin, 83*(5), 880–897. https://doi.org/10.1037/0033-2909.83.5.880.

Prablanc, C., Echallier, J. E., Jeannerod, M., & Komilis, E. (1979). Optimal response of eye and hand motor systems in pointing at a visual target. *Biological Cybernetics, 35,* 113–124. https://doi.org/10.1007/BF00337436.

Proteau, L., Roujoula, A., & Messier, J. (2009). Evidence for continuous processing of visual information in a manual video-aiming task. *Journal of Motor Behavior, 41*(3), 219–231. https://doi.org/10.3200/JMBR.41.3.219-231.

Purves, D., & Lotto, R. B. (2003). *Why we see what we do: An empirical theory of vision.* Sunderland, MA: Sinauer Associates. https://doi.org/10.1162/089892903770007452.

Purves, D., Lotto, R. B., Williams, S. M., Nundy, S., & Yang, Z. (2001). Why we see things the way we do: Evidence for a wholly empirical strategy of vision. *Philosophical Transactions of the Royal Society B: Biological Sciences, 356*(1407), 285–297. https://doi.org/10.1098/rstb.2000.0772.

Sainburg, R. L., & Kalakanis, D. (2000). Dominant and nondominant arm reaching differences in control of limb dynamics during differences in control of limb dynamics during dominant and nondominant arm reaching. *Journal of Neurophysiology, 83*(19), 2661–2675. https://doi.org/10.1109/CBI.2014.52.

Saunders, J. A., & Knill, D. C. (2005). Humans use continuous visual feedback from the hand to control both the direction and distance of pointing movements. *Experimental Brain Research, 162*(4), 458–473. https://doi.org/10.1007/s00221-004-2064-1.

Tremblay, L., Crainic, V. A., de Grosbois, J., Bhattacharjee, A., Kennedy, A., Hansen, S., & Welsh, T. N. (2017). An optimal velocity for online limb-target regulation processes? *Experimental Brain Research, 235*(1), 29–40. https://doi.org/10.1007/s00221-016-4770-x.

Tremblay, L., Hansen, S., Kennedy, A., & Cheng, D. T. (2013). The utility of vision during action: Multiple visuomotor processes? *Journal of Motor Behavior, 45*(2), 91–99. https://doi.org/10.1080/00222895.2012.747483.

van den Tillaar, R., & Ettema, G. (2009). A comparison of overarm throwing with the dominant and nondominant arm in experienced team handball players. *Perceptual and Motor Skills, 109*(1), 315–326. https://doi.org/10.2466/pms.109.1.315-32.

Woodworth, R. S. (1899). The accuracy of voluntary movement. *Psychological Review, 3,* 1–119. https://doi.org/10.1037/h0092992.

Zelaznik, H. N., Hawkins, B., & Kisselburgh, L. (1983). Rapid visual feedback processing in single-aiming movements. *Journal of Motor Behavior, 15*(3), 217–236. https://doi.org/10.1080/00222895.1983.10735298.