RESEARCH ARTICLE

Goal-directed reaching: movement strategies influence the weighting of allocentric and egocentric visual cues

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Abstract The location of an object in peripersonal space can be represented with respect to our body (i.e., egocentric frame of reference) or relative to contextual features and other objects (i.e., allocentric frame of reference). In the current study, we sought to determine whether the frame, or frames, of visual reference supporting motor output is influenced by reach trajectories structured to maximize visual feedback utilization (i.e., controlled online) or structured largely in advance of movement onset via central planning mechanisms (i.e., controlled offline). Reaches were directed to a target embedded in a pictorial illusion (the induced Roelofs effect: IRE) and advanced knowledge of visual feedback was manipulated to influence the nature of reaching control as reported by Zelaznik et al. (J Mot Behav 15:217–236, 1983). When vision could not be predicted in advance of movement onset, trajectories showed primary evidence of an offline mode of control (even when vision was provided) and endpoints demonstrated amplified sensitivity to the illusory (i.e., allocentric) features of the IRE. In contrast, reaches performed with reliable visual feedback evidenced a primarily online mode of control and showed increased visuomotor resistance to the IRE. These findings suggest that the manner a reaching response is structured differentially influences the weighting of allocentric and egocentric visual information. More specifically, when visual feedback is unavailable or unpredictable, the weighting of allocentric visual information for the advanced planning of a reach trajectory is increased.

Keywords Allocentric · Egocentric ·
Induced Roelofs effect · Reaching · Offline · Online

Introduction

When continuous vision is available from the reaching environment (closed-loop reaching: CL), the performer structures their response to take maximal advantage of all available visual feedback. Indeed, reaches performed with concurrent limb and target vision demonstrate more continuous and/or discrete feedback-based limb adjustments and show greater endpoint accuracy and stability than actions performed without vision (Beggs and Howarth 1970; Carlton 1981; Elliott et al. 1999b; Keele 1968; Proteau et al. 1992; Woodworth 1899; see Elliott et al. 2001 for review). These kinematic differences demonstrate that endpoints of CL actions are primarily determined by visually based limb corrections implemented during the trajectory (i.e., online control; e.g., Heath 2005). Notably, Goodale and Milner's (1992; see Goodale et al. 2004 for a more recent review) perception/action model (PAM) asserts that online corrections are subserved by dedicated visuomotor networks residing in the posterior parietal cortex of the dorsal visual pathway (see also Pisella et al. 2000). Moreover, the PAM states that absolute comparisons between the moving limb and the target (i.e., egocentric frame of reference) computed on a moment-to-moment basis are exclusively used to support visuomotor computations in the dorsal visual pathway.

Withdrawing vision at movement onset (open-loop reaching: OL) disrupts the normally online control of action

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and results in trajectories that unfold with few (if any) online corrections and yields amplified endpoint error and instability (e.g., Adamovich et al. 1999; Carlton 1981; Elliott 1988; Heath and Westwood 2003; McIntyre et al. 1997; Westwood et al. 2001, 2003). The aforementioned findings support the claim that the absence of visual feedback elicits a mode of control wherein responses are specified largely in advance of movement onset via central planning mechanisms (i.e., offline control; Heath 2005; Plamondon 1995; Schmidt et al. 1979). Interestingly, although the loss of visual feedback influences the manner a response is structured, the real-time component of the PAM asserts that the nature of the visual information supporting the *planning* of OL actions is the same as the visual information supporting the feedback-based *control* of CL actions. In other words, the visuomotor system uses egocentric cues specified by the dorsal visual pathway to support central planning and ensuing reach kinematics (Westwood and Goodale 2003; see Goodale and Westwood 2004 for review). It is, however, important to note that withdrawing visual feedback disrupts not only the online control of action, but also the preparatory set mediating central planning mechanisms (Heath et al. 2006b; Schluter et al. 1999). Presented in another way, responses are not planned in real-time (i.e., at response cuing); rather, a motor plan is developed prior to movement cuing (i.e., during a preview period) and held in memory until the response is initiated (Elliott and Madalena 1987; Glazebrook et al. 2005; Heath et al. 2004a, 2006b; Heath and Rival 2005; Keetch et al. 2006). Importantly, offline planning of the to-be-executed response would not be supported by egocentric visual cues due to the evanescent nature of dorsal visual processing. Instead, offline planning is thought to access relative and scene-based visual information (i.e., allocentric frame of visual reference) laid down and maintained by the temporally durable perceptual networks of the ventral visual pathway (Hu and Goodale 2000; Westwood et al. 2000; see Milner and Goodale 1995 for details).

An earlier study by our group (Heath et al. 2006a) tested the hypothesis that the manner a response is structured (online versus offline) influences the frame, or frames, of visual reference supporting motor output. Specifically, participants completed grasps to a target object embedded within a Müller-Lyer (ML) figure when CL and OL trials were performed in separate blocks of trials (i.e., blocked feedback schedule) and a condition wherein CL and OL trials were randomly interleaved on a trial-by-trial basis (i.e., random feedback schedule). The logic behind this technique is that responses performed in a random feedback schedule have been shown to be structured primarily offline without feedback-based corrections even when vision is available during the response (Elliott and Allard 1985; Jakobson and Goodale 1991; Khan et al. 2002; Zelaznik

et al. 1983). Thus, our previous study provided a novel basis for determining whether online and offline modes of movement control are differentially influenced by the illusion-evoking (i.e., allocentric) features of the ML figures. CL responses in the blocked feedback schedule showed peak grip apertures that were largely refractory to the ML figures, whereas counterpart responses in the random feedback schedule produced peak grip apertures influenced in a direction consistent with the perceptual effects of the ML figures. Those results were taken as indirect evidence that egocentric cues mediate online control and that allocentric cues in part influence offline action planning.

In the present investigation, we more directly examined whether the manner a response is structured influences the nature of the visual information supporting motor output. Once again, blocked and random feedback schedules were used in combination with actions directed to a pictorial illusion (i.e., the induced Roelofs effect: Bridgeman et al. 1997).[1] Importantly, however, the present study employed a goal-directed reaching, as opposed to grasping, paradigm to directly quantify the manner a response is structured (i.e., online versus offline). We accomplished that objective by computing correlations (R^2 values) relating the spatial position of the limb at early, middle and late stages of the reaching trajectory relative to ultimate movement endpoints. As demonstrated previously, reaches controlled primarily online show modest R^2 values during middle and late stages of reach trajectories due to the evocation of online, feedback-based corrections that nullify errors in the unfolding reaching trajectory (Binsted and Heath 2004; Elliott et al. 1999a; Heath 2005; Heath et al. 2004b; Messier and Kalaska 1999). However, reaches implemented primarily offline elicit more robust R^2 values as the trajectory unfolds without visually derived feedback corrections. In terms of research outcomes, trials involving advanced knowledge that visual feedback will be available during a response should produce the lowest R^2 values (i.e., controlled online) and demonstrate reaching endpoints with enhanced visuomotor resistance to the IRE; that is, access visual information maximizing comparisons between the egocentric position of the limb and the absolute location of a target. In contrast, trials in which visual feedback is withdrawn or cannot be predicted in

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[1] We elected to use the induced Roelofs effect because the illusory features of this stimulus are thought constructed by later visual processing systems (i.e., the ventral visual pathway; see Milner and Dyde 2003 for a discussion of this issue). Moreover, our IRE configuration was oriented in the anteroposterior direction (see Fig. 1) and thus differs from the mediolateral orientation used in most previous work (e.g., Bridgeman et al. 1997, 2000, Dassonville et al. 2004). Importantly, however, the IRE orientation used here has been shown to robustly influence reaching endpoints (Coello et al. 2003; Neely et al. 2007; see Neely 2005 for discussion of IRE orientations and visuomotor susceptibility to allocentric visual cues).
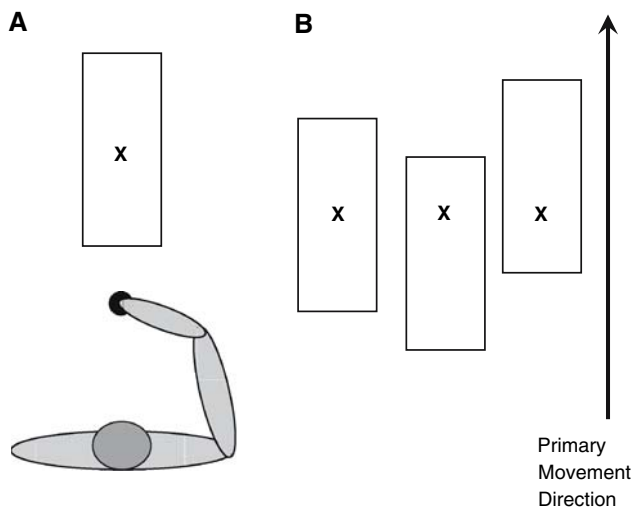
A   **B**

X

X   X   X

Primary
Movement
Direction

Fig. 1 Spatial orientation of the performer relative to the long-axis of the IRE (**a**). The different IRE configurations used in the present investigation (**b**): the center, offset-proximal and offset-distal frames, respectively, from *left* to *right*. Each frame is shown with the middle target location

advance of movement onset should yield amplified R^2 values (i.e., controlled offline) and produce reaching endpoints robustly influenced by the allocentric features of the IRE.

Methods

Participants

Participants were 12 individuals (six males, six females; age range = 18–33 years) from the University of Western Ontario community. All participants had normal or corrected-to-normal vision and signed a consent form approved by the Office of Research Ethics at the University of Western Ontario. This work was conducted in accord with the ethical standards laid down in the 1964 Declaration of Helsinki.

Apparatus

We used an aiming apparatus similar to that introduced by Held and Gottlieb (1958). The apparatus consisted of three shelves supported by an aluminum frame. The top shelf supported an inverted monitor (Dell 1707FP: 8 ms response time), the middle shelf consisted of a one-way mirror and the bottom shelf provided an aiming/reaching surface. The optical geometry of the apparatus created a situation in which the visual stimuli projected by the monitor onto the mirror appeared to participants as being located on the lower/reaching surface of the aiming apparatus. Hence, the participants completed reaching movements to "virtual" targets. A constant optical geometry was maintained via a head/chin rest (Applied Science Laboratories: Bedford,

MA, USA). To prevent direct viewing of the reaching limb, the lights in the experimental suite were extinguished. In the place of veridical limb vision, dual light-emitting diodes (LEDs) attached to a splint complex and secured to the pointing finger (i.e., index finger of right hand) were used to provide instantaneous control of limb vision. All visual and auditory events were controlled via Eprime (version 1.1: Psychology Software Tools, Pittsburgh, PA, USA).

We used the induced Roelofs effect (IRE: Bridgeman et al. 1997) to examine the impact of allocentric cues on motor output. Specifically, from a common home position (i.e., a midline microswitch), participants completed fast and accurate aiming movements to midline targets (i.e., 5 mm "X") embedded within a 14 cm × 6.5 cm rectangle (henceforth referred to as a frame). Visual stimuli were projected in white against a high-contrast black background. For each trial, one of the three targets (18 (near), 20 (middle), 22 (far) cm distal to the home position) was surrounded by one of three frames. The frames used here were centered with respect to the middle target or displaced distally (i.e., offset-distal) or proximally (offset-proximal) by 2 cm relative to the middle target location (Fig. 1). Our group has previously shown that the target and frame configurations used here elicit robust illusory effects on perceptual and motor responses (Neely et al. 2007).

Participants initiated each trial by depressing the home position: that action resulted in the projection of one of the target and frame combinations for 1,000 ms and the concurrent illumination of the LEDs attached to the pointing finger. Following preview, an auditory tone signaled participants to initiate their reaching movement. Reaches were completed in two visual conditions (CL, OL) and two feedback schedules (blocked, random). For CL trials, vision of the limb and target stimuli remained available to participants throughout the trial. For OL trials, vision of the limb and target stimuli was occluded at movement initiation (i.e., release of pressure from the home position). The CL and OL trials described above were completed in a blocked feedback schedule, wherein visual conditions were presented in separate trial blocks: a situation providing advance knowledge of the type of visual feedback available during an upcoming trial. In addition, reaches were completed in a random feedback schedule, wherein CL and OL trials were randomly interleaved on a trial-by-trial basis. In the random feedback schedule, advance knowledge concerning the presence or absence of online visual feedback was not available.

Feedback schedules (blocked and random) were counterbalanced across participants, and in the blocked feedback schedule OL and CL trial blocks were ordered randomly. In both feedback schedules, participants completed 20 trials for each of the visual condition (CL, OL), target distance (near, middle, far) and frame orientation (offset-proximal,

center, offset-distal) combinations. In total, participants completed 720 experimental trials.

Data collection and reduction

In addition to containing LEDs, the splint complex attached to the pointing finger contained an infrared emitting diode (IRED). Following the movement initiation cue, IRED position data were sampled at 200 Hz for 1 s via an OPTOT-RAK 3020 (Northern Digital Inc., Waterloo, ON, Canada). Displacement data were filtered offline via a second-order dual-pass Butterworth filter employing a low-pass cutoff frequency of 15 Hz. Instantaneous velocities were obtained by differentiating displacement data via a five-point central finite difference algorithm. Movement onset was defined as the first frame in which resultant velocity exceeded 50 mm/s for ten consecutive frames (i.e., 50 ms), similarly movement offset was defined as the first of ten consecutive frames in which velocity was less than 50 mm/s.

Dependent variables and statistical analysis

Dependent variables included: reaction time (RT: the time from response cuing to movement onset), movement time (MT: the time from movement onset to movement offset), constant error (CE) in the primary movement direction (i.e., the anteroposterior plane) and its associated variable error (VE) value. To infer the extent reaches were controlled online versus offline, we computed correlations (R^2 values) reflecting the spatial position of the limb at 25, 50 and 75% of MT relative to ultimate movement endpoints. In previous studies (e.g., Binsted and Heath 2004; Heath et al. 2004b, 2007; Krigolson and Heath 2006), our group had demonstrated that reaches controlled primarily online produce weak R^2 values during middle (50%) and late (75%) stages of reach trajectories as early planning errors are attenuated via response-produced visual feedback. In contrast, reaches controlled primarily offline produce more robust R^2 values, as the trajectory unfolds without online modification (see Heath (2005) for details).

In most cases (see exception below), data were examined via two (feedback schedule: blocked, random) by two (visual condition: CL, OL) by three (frame: offset-distal, center, offset-proximal) by three (target: far, middle, near) fully repeated measures ANOVA. Significant main effects/interactions ($P < 0.05$) were decomposed via simple effects and/or power polynomials (alpha = 0.05).

Results

We did not observe any manipulation-related effects for RT (grand mean = 182 ± 8 ms). In terms of MT, a main effect of

target, $F(2, 22) = 104.43$, $P < 0.001$, indicated that MT increased with target eccentricity (only linear effect significant: $F(1, 11) = 114.16$, $P < 0.001$). MT also yielded a significant effect of frame, $F(2, 22) = 5.08$, $P < 0.02$, and a feedback schedule by visual condition by frame interaction, $F(2, 22) = 12.97$, $P < 0.02$. For OL trials (blocked and random), a main effect of frame ($F(2, 22) = 10.16$, $P < 0.001$) showed an increase in MT across the offset-distal (404 ± 17 ms), center (406 ± 17 ms) and offset-proximal (410 ± 18 ms) frame orientations (only linear effect significant: $F(1, 11) = 10.52$, $P < 0.01$). For CL-blocked trials, MTs for offset-distal (408 ± 17 ms), center, (407 ± 18 ms) and offset-proximal (408 ± 18 ms) frame orientations were similar ($P > 0.05$); however, MTs for CL-random trials increased across the offset-distal (402 ± 15 ms), center (405 ± 14 ms) and offset-proximal (409 ± 18 ms) frame orientations (only linear effect significant: $F(1, 11) = 6.55$, $P < 0.01$).

The analysis of CE yielded a main effect of frame, $F(2, 22) = 20.12$, $P < 0.001$, and interactions involving visual condition by frame, $F(2, 22) = 5.92$, $P < 0.01$, and feedback schedule by visual condition by frame, $F(2, 22) = 7.86$, $P < 0.01$. We decomposed the three-way interaction via separate visual condition by frame ANOVAs for each feedback schedule.

Blocked feedback schedule

CE for this feedback schedule produced a main effect of frame ($F(2, 22) = 17.45$, $P < .001$) and a visual condition by frame interaction ($F(2, 22) = 11.65$, $P < .001$). In line with the well-documented perceptual effects of the IRE, overshooting of veridical target location increased linearly across the offset-distal, center, and offset-proximal frame orientations for both CL and OL trials (Fs(2, 22) = 4.98 and 15.65, respectively, Ps < 0.02, only linear effects significant: Fs(1, 11) = 10.56 and 18.23, respectively, Ps < 0.001). Interestingly, however, and as observed in Fig. 2, the nature of the visual condition by frame interaction appears rooted in the fact that CL trials were less influenced by the IRE than OL ones. In support of this assertion, we computed slopes of illusion effects for each participant and found that illusion effects for CL trials (0.27 ± 0.12 mm) were shallower than OL trials (1.70 ± 0.40 mm; $t(11) = -3.99$, $P < 0.02$).

Random feedback schedule

CE in this feedback schedule produced an effect of frame ($F(2, 22) = 11.77$, $P < 0.001$). As with the blocked feedback schedule, overshooting of veridical target location increased across the offset-distal, center and offset-proximal frame orientations (only linear effect significant: $F(1, 11) = 16.35$, $P < 0.01$; Fig. 2). Unlike the blocked feedback schedule, the slopes of individual illusion effects for CL
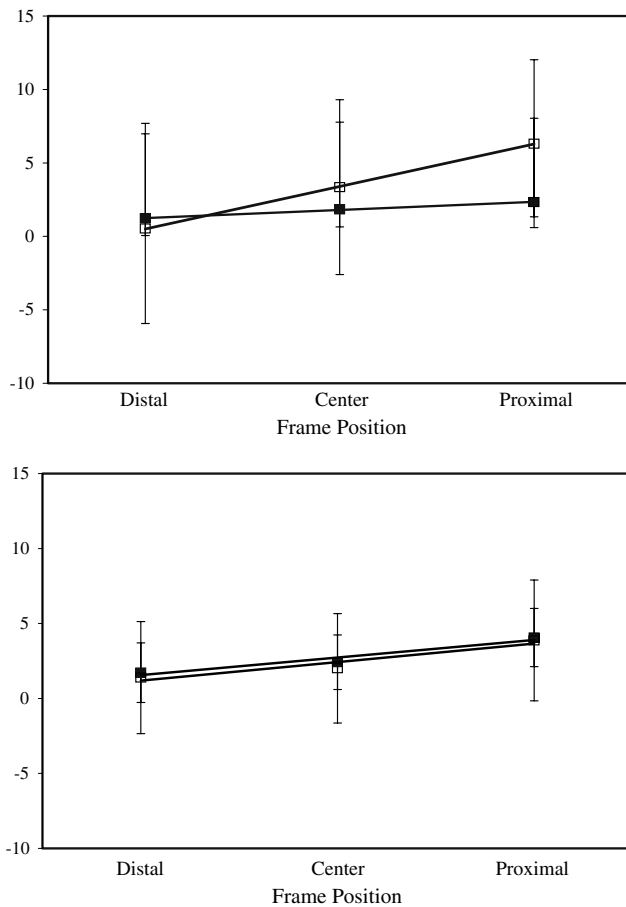
Fig. 2 Constant error (mm) in the primary movement direction in blocked (*top panel*) and random (*bottom panel*) feedback schedules as a function of visual condition (CL = *solid symbols*, OL = *open symbols*) and frame orientation. *Error bars* represent SEM

Fig. 3 The proportion of variance (R^2) explained by the spatial location of the limb (primary reaching direction) at 25, 50 and 75% of MT relative to ultimate movement endpoints as a function of feedback schedule and visual condition. *Error bars* represent SEM

$(0.59 \pm 0.18$ mm) and OL $(0.62 \pm 0.25$ mm) trials did not differ $(t(11) = -0.10, P = 0.92)$.

The results for VE produced a main effect of visual condition, $F(1, 11) = 39.96$, $P < 0.001$, and a feedback schedule by visual condition interaction, $F(1, 11) = 9.58$, $P < 0.01$. The distribution of endpoints for OL-blocked $(11.5 \pm 0.9$ mm) and OL-random $(11.1 \pm 1.50$ mm) trials did not differ $(t(11) = 0.32, P = 0.75)$. For CL trials, a trend was observed such that CL-blocked trials $(5.6 \pm 0.4$ mm) yielded reduced variability relative to CL-random $(8.9 \pm 1.6$ mm) counterparts $(t(11) = -1.78, P = 0.10)$.

Figure 3 shows mean R^2 values of the position of the limb at 25, 50 and 75% of MT relative to ultimate movement endpoints across each of the feedback schedule by visual condition combinations. Notable in this figure is the fact that CL-blocked trials demonstrate reduced spatial correlations relative to CL-random trial counterparts during the middle and late stages of the reach trajectory, whereas OL trials (blocked and random) demonstrated compatible R^2 values.
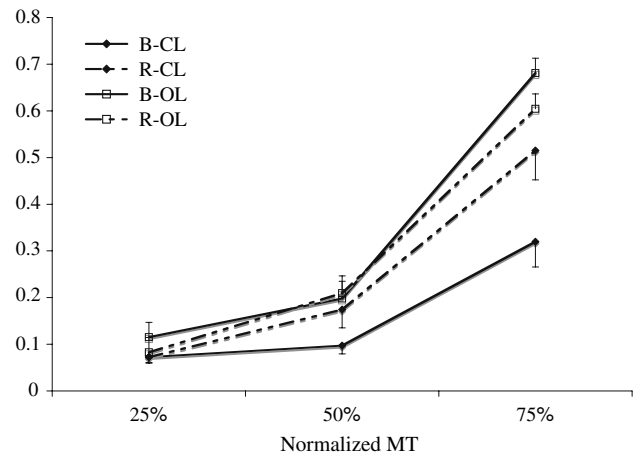
To quantify statistically the R^2 values described just above, we included the factor time (i.e., 25, 50 and 75% of MT) in our ANOVA model. Not surprisingly, R^2 values increased as a function of movement time, $F(2, 22) = 134.05$, $P < 0.001$, and elicited a highest-order interaction involving time, feedback schedule and visual condition, $F(2, 22) = 8.31$, $P < 0.01$. As seen in Fig. 3, no manipulation-related differences were observed at 25% of MT (Ps > 0.05). At 50 and 75% of MT, values for OL-blocked and OL-random trials did not differ (Ps > 0.05); however, during that same time frame CL-blocked trials produced lower values than CL-random counterparts (ts(11) = 6.82 and 10.75, respectively, for 50 and 75%, Ps < 0.01).

Discussion

Feedback schedules influence reaching strategies

The predicted availability of visual feedback has been shown to influence the manner in which actions are structured. In particular, CL reaches performed in a predictable environment show effective (i.e., accurate) and stable endpoints relative to counterparts performed in an unpredictable environment (Elliott and Allard 1985; Khan et al. 2002; Zelaznik et al. 1983). Moreover, grasp trajectories are more efficient (i.e., smaller maximal grip apertures) when visual feedback can be predicted in advance of movement onset (Heath et al. 2006a; Jakobson and Goodale 1991). Such findings have been interpreted as evidence that performers adopt distinct modes of movement control dependent on advanced knowledge of visual feedback. Thus, when faced with a blocked feedback schedule, partic-

ipants structure responses online to take maximal advantage of visual feedback to attenuate early planning errors. In a random feedback schedule, however, visuomotor uncertainty engenders the adoption of a primarily offline mode of control wherein responses are structured largely in advance of movement onset and visual feedback is not used for trajectory modifications—even when available during a response.

Our analysis of reach trajectories extends previous work manipulating feedback schedules by directly showing that the predicted availability of visual feedback influenced the manner in which responses were structured. We found that CL-blocked trials yielded lower R^2 values than CL-random counterparts (i.e., at 50 and 75% of MT),[2] whereas R^2 values for OL trials were not influenced by the different feedback schedules. What is more, Fig. 3 shows that R^2 values for CL-random trials were more characteristic of OL (blocked and random) trials than CL-blocked ones. Based on previous work (e.g., Binsted and Heath 2004; Elliott et al. 1999a; Heath 2005; Heath et al. 2004b), we propose that the spatial correlations observed here evidences two modes of reaching control. Specifically, we assert that the lower R^2 values of CL-blocked trials reflect an online mode of control, wherein initial planning errors are reliably attenuated during the reach trajectory via visually based limb corrections. In contrast, the amplified R^2 values characterizing CL-random trials and OL-blocked and OL-random trials are taken to reflect an offline mode of control, wherein trajectories are specified primarily in advance of movement onset via central planning mechanisms. Moreover, the fact that CL-random as well as OL-blocked and OL-random trials elicited heightened endpoint variability relative to CL-blocked trials supports the assertion that reaches in the former conditions (i.e., CL-random, OL-blocked, OL-random) relied on a similar representation to support offline movement planning processes (see also Khan et al. 2002).

Reaching strategies and the integration of allocentric visual cues

A recent extension of the PAM states that metrical visual information specified in an egocentric frame of visual reference supports motor output when visual information is available to the performer at the time of response planning (so-called real-time control; Westwood and Goodale 2003; see Goodale et al. 2004 for review). Indeed, the PAM

asserts that motor output is influenced by allocentric visual cues only when a response is initiated after a period of visual delay (e.g., Hu et al. 1999; Hu and Goodale 2000; Westwood et al. 2000). According to the PAM then, endpoints across the feedback schedule and visual condition combinations studied here should have demonstrated visuomotor resistance to the IRE because in all cases direct visual information was available to the performer at the time of response planning. The present findings, however, did not bear out that prediction. Endpoints for all feedback schedule and visual condition combinations were influenced in a direction consistent with the perceptual effects of the IRE (e.g., Bridgeman et al. 1997; Neely et al. 2007). Thus, endpoints for the offset-proximal frame overshot target location more than the offset-distal frame (cf. Coello et al. 2003; Neely et al. 2007). It is, however, important to note that the degree to which actions were "tricked" by the IRE was influenced by an interaction between feedback schedule and visual condition. Specifically, CL and OL trials in the random feedback condition showed a comparable (and robust) influence of the IRE, whereas the magnitude of illusion effects in CL-blocked trials was less than counterpart OL-blocked trials. Further, examination of individual illusion effects showed that slopes of CL-blocked trials were shallower than the other feedback schedule and visual condition combinations. What is more, movement times for CL-blocked trials were not influenced by the IRE, whereas movement times increased linearly across offset-distal to offset-proximal frames in the other feedback schedule and visual condition combinations. Put another way, the spatial features of reach trajectories were less sensitive—and temporal features were refractory—to the allocentric features of the IRE when feedback could be predicted prior to movement onset (i.e., the CL-blocked trials). In contrast, spatial and temporal parameters of reach trajectories were more markedly influenced by the IRE when visual feedback was not available (i.e., OL-blocked, OL-random) or could not be predicted in advance of movement onset (i.e., CL-random).

In a previous study, our group showed that maximal apertures of CL grasps were largely refractory to ML figures when performed in a blocked as compared to random feedback schedule (Heath et al. 2006a). Those findings were taken as indirect evidence that CL-blocked grasps are controlled online and mediated via egocentric visual information, whereas CL-random grasps are controlled offline and supported via allocentric visual cues. Of course, in the present investigation we provide a more direct examination of the aforementioned proposal given our contemporaneous examination of trajectory profiles (R^2 values) and endpoint accuracy. In this investigation, we are therefore able to comment more directly on whether a specific mode of movement control is differentially influenced by a distinct

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[2] The fact that R^2 values at 25% of movement time did not differentiate between the feedback schedule and visual condition combinations is congruent with earlier work arguing that at this time point the spatio-temporal features of an initial movement impulse do not have sufficient time to unfold to predict ultimate movement endpoints (see Heath et al. 2004b).

frame, or frames of visual reference. Here, we show that CL-blocked reaches yielded the lowest R^2 values (i.e., reaches were controlled online) and were most resistant to the IRE. In contrast, CL-random, OL-blocked and OL-random reaches showed amplified R^2 values (i.e., reaches were controlled offline) and demonstrated enhanced illusory effects on endpoint accuracy and overall movement durations. Thus, our data extend the claim that the manner an action is structured influences the nature of the visual information supporting motor output; that is, reaches controlled online are supported primarily via egocentric visual cues and reaches controlled offline are more strongly influenced by allocentric visual cues.

The weighting of allocentric and egocentric cues for visuomotor control

An issue requiring redress is why the online and offline modes of control identified here were differentially reliant on allocentric and egocentric visual cues. In other words, why were reaches controlled offline "tricked" to a greater degree by the IRE than reaches controlled more online? One congruent explanation is that in an offline mode of control participants deliberately precompute the parameters of an upcoming response during an initial preview period and hold that motor plan in memory until response cuing (Henry 1986; Henry and Rogers 1960; see also Smyrnis et al. 1992). Structuring a response in advance of movement onset would entail obligatory visual processing and would thus more heavily weight allocentric cues in the sensorimotor transformations underlying the to-be-completed response (Heath et al. 2004a; Heath and Rival 2005). In terms of online control, a myriad of studies have shown that reaching accuracy is heightened when participants are afforded direct visual contact with their moving limb and target object (Carlton 1981; Elliott et al. 1999b, 2001 for review; Meyer et al. 1988; Woodworth 1899) and that the initial kinematics of the response are structured at the time of response cuing and not before (Klapp 1975). Of course, such a mode of control would heavily weight egocentric visual information because direct limb/target comparisons are reliably available for online limb adjustments (Smeets et al. 2002). It is, however, clear from the present results that reaches controlled online were not served by exclusive egocentric visual cues because the contextual features of the IRE influenced movement endpoints, albeit to a lesser magnitude than actions controlled offline (cf. Heath et al. 2005). This finding is in line with a growing number of studies indicating that allocentric visual information derived from illusory arrays (e.g., Coello et al. 2003; Elliott and Lee 1995; Daprati and Gentilucci 1997; Gentilucci et al. 1996; Heath et al. 2007; Mendoza et al. 2006; see Mendoza et al. 2005 for review of this issue), non-illusory

geometric features (e.g., Coello and Grealy 1997; Conti and Beaubaton 1980; Krigolson and Heath 2004; Krigolson et al. 2007; Redon and Hay 2005; Velay and Beaubaton 1986) and non-target visual landmarks (Diedrichsen et al. 2004; Obhi and Goodale 2005) can influence real-time movement planning processes as well as feedback-based limb adjustments. Indeed, it may be that the higher spatial frequencies associated with a target embedded in a structured visual environment (i.e., the frame in the present study) affords salient visual landmarks thereby resulting in the integration of allocentric cues for online limb corrections (Krigolson et al. 2007; see also Whitney et al. 2003). We therefore propose that when vision of the limb and target are concurrently available, online control is mediated by interacting egocentric and allocentric cues, with an increased weighting of egocentric cues due to their salience for online corrections. In contrast, visuomotor control mechanisms adjust to deficiencies in egocentric information (e.g., when limb and/or target information is unavailable or unreliable) by structuring movements in advance of movement onset and increasing reliance on temporally stable allocentric cues.[3]

Two final issues require address. The first relates to the impact of the IRE across the reaching conditions studied here. Previous work by Bridgeman and colleagues (Bridgeman et al. 1997, 2000; Dassonville et al. 2004) report that "immediate jabbing movements" are impervious to the illusory properties of the IRE.[4] In that work, the long-axis of the frame surrounding the target was oriented mediolateral to the participant's viewing perspective. Other work, however, has proposed that visuomotor sensitivity to the IRE is dependent on the orientation of the frame surrounding the target. Specifically, Coello et al. (2003) found a reliable effect of the IRE when the long-axis of the frame surrounding the target was oriented in an anteroposterior fashion. In addition, recent work by our group (Neely et al. 2007; see also Neely 2005) has shown that the weighting of allocentric cues is amplified under an anteroposterior relative to

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[3] Of course, the hypothesis proposed here is specific to situations in which reaching/grasping responses are directed to a target within a structured visual background and not restrictive experimental contexts wherein allocentric visual cues are not available to the performer; e.g., when a performer reaches to an isolated target (i.e., point of light) presented in an otherwise neutral or empty visual background.

[4] Bridgeman et al's (1997) original IRE experiment is frequently cited as providing direct evidence that the IRE does not influence visuomotor control. Careful examination of that experiment, however (see Experiment 1), shows that "5 subjects showed a highly significant Roelofs effect [$F(2, 4) > 18$, $P < 0.01$], whereas the other 5 showed no sign of an effect [$F(2, 4) \leq 3.16$, $P > 0.18$]" (p. 460). Importantly, that finding combined with a more recent work (Neely et al. 2007) highlights the existence of a controversy surrounding the extent to which the IRE represents an exemplar illusion supporting the view that egocentric visual cues restrictively mediate visually derived reaches.

mediolateral IRE orientation. Thus, results from the current study (which employed an anteroposterior IRE orientation) are congruent with other work suggesting that illusory cues of the IRE influence the coding of movement distance to a greater degree than computations supporting the specification of movement direction (see Coello et al. 2003; Neely et al. 2007).

The final issue to be addressed is where in the central nervous system might egocentric and allocentric visual cues interact to influence motor output. Indeed, extensive neuropsychological and neuroimaging work suggest that the dorsal and ventral visual pathways, respectively, mediate egocentric and allocentric representations of visual space (e.g., James et al. 2003; Culham et al. 2003; see Milner and Goodale 1995). It is, however, important to note that recent work in the optic ataxia literature has shown that individuals with lesions to the posterior parietal cortex do not build into their reach trajectories allocentric visual information important for obstacle avoidance (Schindler et al. 2004). In this context, Schindler et al. assert that visuomotor networks in the dorsal visual pathway directly integrate allocentric cues for the control of reach trajectories (see also McIntosh et al. 2004). Alternatively, it is possible that allocentric visual cues indirectly influence motor output via the extensive interconnections between the dorsal and ventral streams (Merigan and Maunsell 1993) or by bypassing the dorsal stream entirely and influencing motor areas through projections to the prefrontal cortex (Ungerleider et al. 1998). Notably, the idea that allocentric cues may directly or indirectly influence visuomotor processes provides a framework for understanding the differential weighting of egocentric and allocentric visual cues and thus may account for the pattern of online and offline control-derived illusory effects reported here (see Binsted et al. 2007).

Conclusions

It is proposed that advanced knowledge that visual information will be available during a goal-directed reaching task evokes an online mode of control mediated primarily via egocentric visual cues. When visual information is unavailable or unreliable, however, it is proposed that participants adopt a more offline mode of control wherein allocentric visual cues are more heavily weighted (relative to online control) to support the spatiotemporal features of the to-be-completed reach trajectory.

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