Allocentric Visual Cues Influence Online Limb Adjustments

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The present investigation sought to examine the nature of the visual information supporting online movement corrections. Participants were instructed to maintain gaze on the veridical endpoint of a neutral Müller-Lyer (ML) configuration in advance and during reaches performed with and without continuous limb vision. At movement onset, the stimulus array remained either the same (i.e., the neutral ML figure) or was perturbed to a fins-in or fins-out ML configuration. We reasoned that our illusion-based paradigm would provide a novel basis to examine the nature of the visual information supporting online movement corrections without the intrusion of putative biased ocular/manual motor interactions. Early reaching kinematics were refractory to the illusion-based perturbation; however, later kinematics were influenced in a direction consistent with the well-documented perceptual effects of the ML illusion. This illusory bias was present irrespective of the presence or absence of limb vision and the corollary extent reaches were controlled online. These results counter the view that metrical visual information specified in an egocentric frame of reference supports online movement corrections (e.g., Glover, 2004). Instead, the present results suggest online movement control is subserved by visual input specified via interacting egocentric and allocentric reference frames.

Key Words: illusions, Müller-Lyer, online corrections, reaching, visually guided

An influential model of visuomotor control (the perception/action model: PAM) holds that metrically precise (i.e., Euclidean) visual information specified in an egocentric frame of visual reference mediates online limb adjustments (Milner & Goodale, 1995). In support of this position, a number of studies have shown visually guided reaching and grasping movements to be mostly—if not entirely—refractory to the illusion-inducing elements of pictorial illusions (Bridgeman, Perry, & Anand, 1997; Aglioti, De Souza, & Goodale, 1995; Brenner & Smeets, 1996; Heath, Rival, Westwood, & Neely, 2005; Jackson & Shaw, 2000; Westwood, Heath, & Roy, 2000). In a similar vein, Glover's planning/control model (PCM: Glover, 2004) asserts that the planning or perception-based influences of pictorial illusions are resolved

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via the integration of metrical visual information for online limb corrections (see Glover & Dixon, 2001).[1]

Conversely, a more limited—but growing—body of evidence indicates that reaching and grasping movements are "tricked" by pictorial illusions (e.g., Elliott & Lee, 1995; Daprati & Gentilucci, 1997; Gentilucci, Chieffi, Daprati, Saetti, & Toni, 1996; Westwood, McEachern, & Roy, 2001b). These findings counter the PAM and PCM and instead suggest that unitary visual input entailing aggregation of egocentric and allocentric visual cues (i.e., scene-based cues surrounding a target) specifies target location in peripersonal space (Franz, 2003). Importantly, however, the just mentioned work did not explicitly quantify the extent that central planning and/or online control processes contributed to the biased reaching trajectory (e.g., Woodworth, 1899; see Elliott, Helsen, & Chua, 2001 for review of two-component reaching models). This represents an intriguing question because recent work by Heath and colleagues (Heath & Rival, 2005; Heath, Rival, & Binsted, 2004a; Heath, Rival, & Neely, 2006a; Heath, Rival, Neely, & Krigolson, 2006b) has shown that the extent reaches are planned primarily in advance of movement onset (i.e., so-called offline control) or controlled primarily via real-time limb adjustments (so-called online control) influences the degree allocentric visual cues influence movement trajectories.

One method recently employed to assess the nature of the visual information supporting online movement corrections entails an illusion-based perturbation. In this paradigm, a preview object presented in an otherwise neutral visual background is unexpectedly altered at movement onset to produce an illusory configuration. For example, inward or outward pointing fins added to a horizontal line produce an "online" Müller-Lyer (ML) illusion (Mendoza, Elliott, Meegan, Lyons, & Welsh, 2006; see also Handlovsky, Hansen, Lee, & Elliott, 2004). Bearing in mind that the addition of illusory context does not impact veridical movement endpoint, Mendoza et al. found that the location of the limb at peak deceleration as well as ultimate reaching endpoints were biased in a direction consistent with the perceptual effects of the ML figures. Owing to the fact that illusory information was revealed after movement onset and the observation that illusory effects were limited to movement deceleration, these results indicate that allocentric visual cues influence online movement corrections.

In the present investigation, we employed ML figures in an illusion-based perturbation similar to that of Mendoza et al. (2006) with two notable exceptions. First, the present investigation required participants to maintain their gaze on the veridical endpoint of a neutral preview object (i.e., horizontal line presented in an empty visual background) in advance and during the completion of visually guided reaching movements. In contrast, participants in the Mendoza et al. study implemented concomitant saccadic and manual responses at movement onset. Our manipulation is motivated by work showing that biased oculomotor signals shape (or at least influence) manual motor output (Lavrysen et al., 2006; Soechting, Engel, & Flanders, 2001; see also Engel, Anderson, & Soechting, 2000) and the report that reaches performed without a contemporaneous saccade are less influenced by illusory (i.e., allocentric) visual context (Gentilucci, Daprati, Gagitano, & Toni, 1997; but see Binsted & Elliott, 1999).

A second issue to be addressed is the relative weighting of egocentric and allocentric visual cues when vision of the limb is available or unavailable during the

response. Indeed, continuous visual input from the limb has been shown to produce reaches that are more accurate and less variable than their limb occluded counterparts (e.g., Berkinblit, Fookson, Smetanin, Adamovich, & Poizner, 1995; Carlton, 1981; Elliott al., 1999; Heath, Westwood, & Binsted, 2004b). As well, Gentilucci et al. (1997) found that reaches to the vertex of visible ML figures elicited greater visuomotor resistance under a limb visible than a limb occluded condition (see also de Grave, Brenner, & Smeets, 2004). These results contend egocentric visual cues are weighted more heavily during actions wherein continuous limb vision is available. In the present investigation therefore, we manipulated limb vision in an illusion-based perturbation paradigm to examine if the presence or absence of ego-motion signals influences the nature of visual information supporting online movement corrections.

Methods

Participants

Twenty-three participants from the Indiana University community volunteered for this experiment (age range: 21-24 years). Participants reported normal or corrected-to-normal vision (via contact lenses only) and were right-handed as determined by a modified version of the University of Waterloo Handedness questionnaire (Bryden, 1977). Participants signed a consent form in accord with the guidelines of the Office of Human Research, Indiana University and this study was conducted in accordance 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 was placed on a normal tabletop and consisted of a rectangular box (74 cm high, 96 cm wide, 60 cm deep) divided in half by a one-way mirror. A 17-inch LCD computer monitor (NEC Multisync model 1765: 16 ms response rate) was placed upside down on the upper shelf of the apparatus to project visual stimuli on the surface of the mirror. The difference between the height of the upper shelf and the mirror, and the mirror and the lower/reaching surface of the aiming apparatus was constant (i.e., 37 cm); hence, visual stimuli projected onto the mirror appeared on the lower surface of the aiming apparatus (i.e., below the mirror). Participants sat at an open end of the apparatus and completed pointing movements to virtual targets that appeared to participants as being on the lower/reaching surface of the apparatus. A constant optical geometry was maintained via a head-chin rest (Lafayette Instruments, model 14302, Lafayette, IN).

Participants completed reaching movements with their right hand (specifically their right index finger) from a common home position (i.e., a microswitch located 8.5 cm to the left of participants midline and 25 cm from the front edge of the table surface) to the right vertex of fins-in, control, and fins-out ML figures. The long axis of ML figures was oriented mediolateral to participants with the left vertex of each figure 5 cm to the right of the home position and 25 cm from the front edge of the tabletop. The vertex-to-vertex distances used here were 9 and 11.5 cm (~11

and 15 degrees of visual angle), thus, reaching to touch the vertex required 14 and 16.5 cm of respective left to right limb displacement. Fin angles for the fins-in (<--->) and fins-out (>---<) figures were 30 degrees. The control figure consisted of only a horizontal line.

To prevent direct viewing of the limb, the lights in the experimental suite were extinguished. In the place of the veridical limb, dual light emitting diodes (red LEDs) attached to a splint complex and secured to the tip of the index finger (i.e., the pointing figure) provided visual feedback about limb position. Eprime (version 1.0) was used to present and control visual and auditory events.

Procedure

Two trial conditions (experimental and control) and two visual conditions (limb visible, limb occluded) were used in this investigation and factorially combined to produce four separate blocks of trials randomly presented to participants. In each trial block participants were instructed to point to the right vertex of ML figures as "quickly and accurately as possible." A trial began once the limb depressed the home position microswitch. That action illuminated the LEDs attached to the limb. For limb visible trials, the LEDs remained visible throughout the duration of a trial, whereas the LEDs were extinguished coincident with the onset of a pointing response during limb occluded trials (i.e., release of pressure from the home position microswitch). Hence, in the latter condition online limb vision was occluded during response execution.

During control trials, depressing the home position microswitch, in addition to illuminating the LEDs, resulted in the projection of one of the six stimulus configurations (i.e., 9 cm fins-in, control, and fins-out figure and 11.5 cm fins-in, control, and fins-out figure) for a 2,500 ms preview phase. During the preview phase, participants were instructed to direct and maintain their gaze on the right vertex of the stimulus (i.e., the veridical movement endpoint). Following preview, participants received an auditory tone instructing them to initiate their pointing movement. Participants completed an equal number of reaches to each stimulus configuration for a total of 240 control trials. Stimulus configuration was ordered pseudo-randomly.

In the experimental trials, the same general procedures as just described were employed with two notable exceptions. First, the 9 or 11.5 cm control ML figure was presented during preview. Second, during 66% of experimental trials a target perturbation occurred at movement onset. Specifically, for 33% of experimental trials the control figure presented during preview also served as the target during the pointing response, whereas the remaining 66% of experimental trials entailed a stimulus perturbation once the limb broke contact with the home position. For one half of the perturbation trials, the control figure was replaced with the appropriately sized fins-in figure, and on the other half, the control figure was replaced with the appropriately sized fins-out figure. Notably, this illusion-based perturbation did not alter veridical movement endpoint. Participants completed 240 trials in the experimental block; hence, the number of trials to the 9 and 11.5 cm fins-in, control, and fins-out figures corresponds to the number of trials performed to the same stimulus configurations during the block of control trials. The ordering of the preview object (i.e., 9 and 11.5 cm control figure) as well as the ordering of stimulus perturbation was pseudo-randomized.

Data Collection and Reduction

In addition to containing dual LEDs, the splint complex included an infra-red emitting diode (IRED). IRED data were sampled at 200 Hz for 1 s following onset of the auditory initiation tone via an OPTOTRAK 3020 (NDI, Waterloo, ON). Off-line, we filtered displacement data via a second-order dual-pass Butterworth filter employing a low-pass cut-off frequency of 15 Hz. Instantaneous velocities were computed by differentiating displacement data via a three-point central finite difference algorithm. Velocity data were again differentiated to obtain acceleration.

To ensure that participants maintained gaze during a trial, a camcorder (Sony model TR42, 8 mm) operating in high-speed mode (60 Hz) was used to provide up close images of participants eyes. We monitored the video online via a 13-inch Toshiba color CRT. Trials in which we detected an eye movement during the response were excluded from further data analysis and accounted for no more than 1% of the trials for any participant.

## Dependent Variables and Statistical Analysis

The frame associated with movement onset was marked by an analog signal driven by the home position microswitch (i.e., release of pressure from the microswitch). Movement offset was the frame at which resultant velocity fell below 50 mm/s for 10 consecutive frames (i.e., 50 ms). Dependent variables included: reaction time (RT: time between response cuing and movement onset), movement time (MT: time between movement onset and offset), peak velocity (PV: maximum resultant velocity between movement onset and offset), time to peak velocity (TPV: time between movement onset and maximum resultant velocity), and time after peak velocity (TAPV: time between maximum resultant velocity and movement offset). In addition, spatial displacement of the limb from the home position was computed in the primary movement direction at peak acceleration (PA: maximum resultant acceleration between movement onset and movement offset), PV, peak deceleration (PD: maximum resultant deceleration between movement onset and movement offset) and the end of the response (END: position of the limb at movement offset). Last, we computed the proportion of variance (R^2) explained by the spatial position of the limb in the primary movement direction at PA, PV, and PD relative to ultimate movement endpoints. The logic behind this technique is that reaches controlled more online should produce lower R^2 values as the unfolding trajectory is modified to attenuate early planning errors (see Heath, 2005 for complete details).

An alpha level of 0.05 was used to interpret all omnibus tests. In most cases (see exceptions below) data were examined via 2 (block: experimental, control) × 2 (limb vision: limb visible, limb occluded) × 2 (target: 9 cm, 11.5 cm) × 3 (illusion: fins-in, control, fins-out) repeated measures ANOVA. When appropriate, F-statistics were corrected for violations of the sphericity assumption using the appropriate Huynh-Feldt correction (corrected degrees of freedom reported to one decimal place). Significant effects and interactions were decomposed via simple effects analyses.

Results

Performance and Kinematic Measures of Movement Timing

RTs were not influenced by the different experimental manipulations (grand mean = 206 ± 6 ms). For MT, limb visible trials (421 ± 21 ms) were longer than limb occluded trials (378 ± 21 ms), $F(1, 22) = 18.69$, $p < .001$, and MTs increased with target length, $F(1, 22) = 57.75$, $p < .001$. Additionally, an effect for illusion, $F(2, 44) = 9.09$, $p < .001$, indicated the fins-in figures elicited shorter MTs than the control figures [$t(22) = 3.23$, $p < .01$], in turn the control figures produced shorter MTs than the fins-out figures [$t(22) = 2.20$, $p < .05$) (Figure 1).
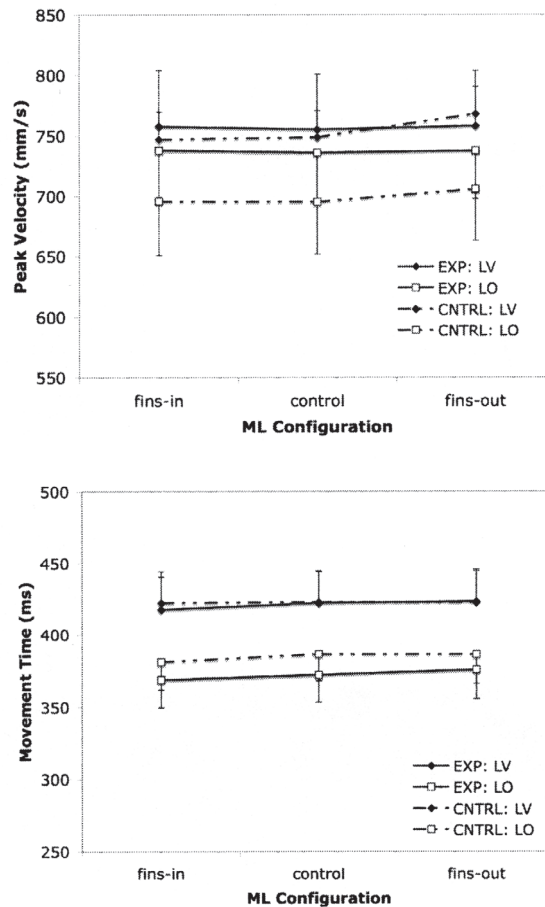
Figure 1—Peak velocity (mm/s: upper panel) and movement time (ms: lower panel) as a function of trial block (experimental, control), limb condition (limb visible, limb occluded) and ML configuration (fins-in, control, fins-out).

PVs for limb visible trials (755 ± 40 mm/s) were greater than limb occluded trials (717 ± 40 mm/s), $F(1, 22) = 7.60$, $p < .02$, and PVs increased with target length, $F(1, 22) = 120.87$, $p < .001$. In addition, PV produced an effect of illusion, $F(2, 44) = 15.20$, $p < .001$, and a block by illusion interaction, $F(2, 44) = 5.70$, $p < .01$. As shown in Figure 1, PVs during experimental trials did not vary as a function of ML configuration [$F(2, 44) = 0.60$, $p > .05$; b = 0.01 mm/s]. For the
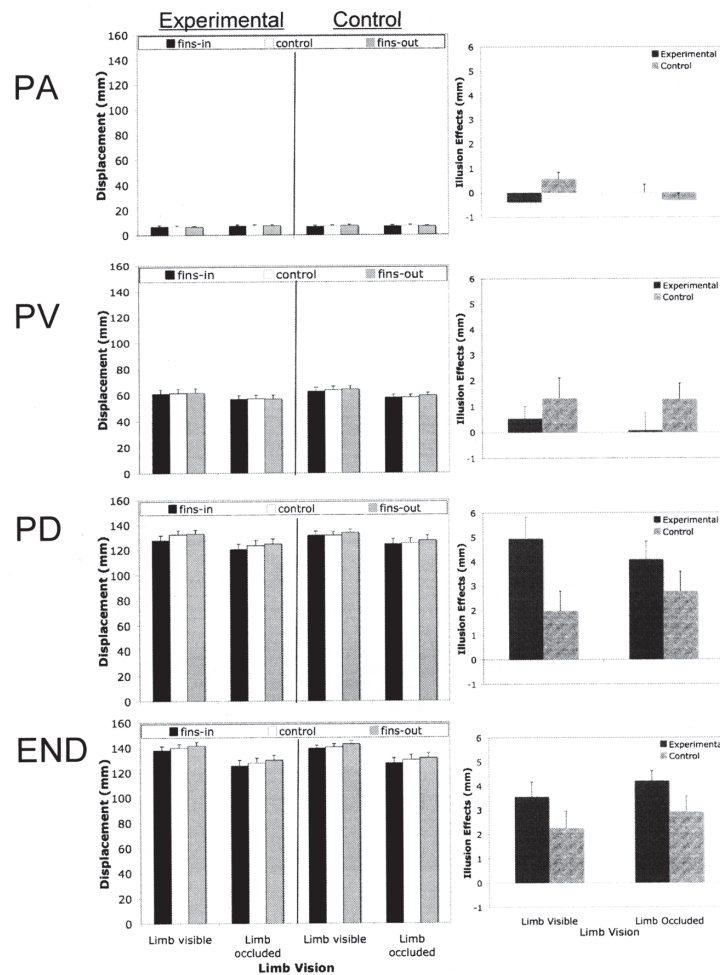
Figure 2—Limb displacement (mm) in the primary movement axis is depicted for peak acceleration (PA), peak velocity (PV), peak deceleration (PD), and movement endpoint (END) as a function of trial block (experimental, control), limb condition (limb visible, limb occluded) and ML configuration (fins-in, control, fins-out). In addition side panels for associated kinematic markers depict illusion effects (fins-out figure minus fins-in figure: mm) as a function of trial block and limb condition.

control trials, however, a significant impact of illusion was observed [$F(2, 44) =$ 12.55, $p < .001$; b = 7.8 mm/s]: fins-in and control figures did not differ [$t(22) =$ 0.23, $p > .05$); however, control figures elicited lower PVs than fins-out figures ($t(22) = 4.14$, $p < .001$. Analysis of TPV indicated the time to PV increased with target length, $F(1, 22) = 36.78$, $p < .001$. In turn, TAPV showed that movement deceleration increased with target length, $F(1, 22) = 21.31$, $p < .001$, and TAPV was longer for limb visible (256 ± 19 ms) than limb occluded (215 ± 15 ms) trials, $F(1, 22) = 21.31$, $p < .001$.

Spatial Displacement of Reaching Trajectories

Limb displacement in the primary movement direction was examined via 4 (marker: PA, PV, PD, END) × 2 (block: experimental, control) × 2 (limb vision: limb visible, limb occluded) × 2 (target: 9 cm, 11.5 cm) × 3 (illusion: fins-in, control, fins-out) repeated measures ANOVA.[2] This analysis yielded effects for marker, $F(1.8, 40.3) = 1100.52$, $p < .001$, limb vision, $F(1, 22) = 16.21$, $p < .01$, illusion, $F(2, 44) = 35.73$, $p < .001$, target, $F(1, 22) = 243.55$, $p < .001$, as well as interactions involving marker by limb vision, $F(1.6, 37.2) = 10.06$, $p < .001$, marker by illusion $F(5.2, 115.7) = 17.08$, $p < .001$, marker by target, $F(1.5, 36.5) = 220.85$, $p < .001$, and marker by block by illusion, $F(5.4, 119.5) = 7.45$, $p < .001$). To decompose the interactions outlined above, we elected to examine the impact of block, limb, illusion, and target separately for each kinematic marker. At PA, no significant main effects or interactions were observed (p values > 0.05). At PV through END, limb displacement was influenced by target length [F values (1, 22) = 119.57, 271.25, and 266.16, respectively, p values < .001]. In terms of the impact of illusion, control trials were not influenced by the ML figures at PA [$F(2, 44) = 0.31$, $p > .05$] but did scale in relation to the perceptual effects of the ML figures from PV to END [F values (2, 44) = 4.56, 14.05, and 30.18, respectively, p values < .02]. For the experimental trials, limb displacement was refractory to the ML figures at PA and PV [F values (2, 44) = 0.54 and 2.98, respectively, $p > .05$), but not from PD to END [F values (2, 44) = 27.06 and 30.18, respectively, p values < .001) (see Table 1 and Figure 2).

We also computed illusion effects (fins-out figure minus fins-in figure) separately for each participant at each kinematic marker. Illusion effects were subjected to 4 (PA, PV, PD, END) × 2 (block: experimental, control) × 2 (limb vision: limb visible, limb occluded) repeated measures ANOVA. This analysis produced a significant effect of marker, $F(3, 66) = 31.42$, $p < .001$, block, $F(1, 22) = 4.55$, $p < .05$, and a marker × block interaction, $F(3, 66) = 5.04$, $p < .01$. Illusion effects increased from PA until PD and then plateaued. Illusion effects for experimental and control trials were similar at PA and PV [t values (22) = –1.40 and 1.34, respectively, p values > .05] but were larger for experimental trials at PD and END [t values (22) = 3.44 and 2.56, respectively, p values < .02) (see Figure 2).

Proportion of Endpoint Variance (R^2) Explained at PV and PD

We computed spatial correlations at discrete stages in the reaching trajectories to determine if our experimental manipulations influenced how participants controlled

Table 1 Spatial Displacement of the Limb (mm) at Peak Acceleration (PA), Peak Velocity (PV), Peak Deceleration (PD), and Movement Endpoint (END) as a Function of Stimulus Configuration Across Experimental and Control Trials

Kinematic Marker/ Experimental Block	ML configuration			t-tests
	fins-in	control	fins-out	
PA				
Experimental	7.1 (0.8)	7.0 (0.8)	6.9 (0.8)	fins-in = control = fins-out
Control	7.0 (0.7)	7.1 (0.7)	7.1 (0.7)	fins-in = control = fins-out
PV:				
Experimental	58.9 (2.8)	59.1 (2.8)	59.1 (3.0)	fins-in = control = fins-out
Control	60.3 (2.4)	60.8 (2.4)	61.6 (2.4)	fins-in = control = fins-out
PD:				
Experimental	124.2 (3.8)	127.8 (3.7)	128.7 (4.0)	fins-in < control < fins-out
Control	128.1 (3.5)	129.2 (3.5)	130.5 (3.7)	fins-in < control < fins-out
END:				
Experimental	131.7 (3.5)	133.6 (3.5)	135.6 (3.5)	fins-in < control < fins-out
Control	134.4 (3.1)	135.2 (3.1)	137.0 (3.2)	fins-in < control < fins-out

Note. Values in parentheses represent *SEM*. Specific *t*-test contrasts are found in the far right column.

their reaches. Figure 3 (outside panels) illustrates an exemplar participant reaching to the 9 cm control ML figure during experimental and control trials with and without limb vision. From this figure it can be observed that spatial correlations generally increased across kinematic markers (i.e., from PA to PV) and did not vary as a function of experimental and control trials. In addition, late in reaching trajectory (i.e., PV to PD) the spatial correlations for limb visible trials were less than their limb occluded counterparts: a result indicative of greater online control when limb vision was available.

Group analysis of spatial correlations mirrored the description above. Specifically, we submitted R^2 values to 3 (marker: PA, PV, PD) × 2 (block: experimental, control) × 2 (limb: limb visible, limb occluded) × 3 (illusion: fins-in, control, fins-out) × 2 (target: 9 cm, 11.5 cm) repeated-measures ANOVA. This analysis produced main effects for marker, $F(1.1, 24.9) = 73.07$, $p < .001$, and limb, $F(1, 22) = 49.06$, $p < .001$, as well as a marker by limb interaction, $F(1.2, 27.3) = 31.14$, $p < .001$. R^2 values increased from PA through PD and limb visible and limb occluded trials yielded similar spatial correlations early in the movement (i.e., at PA: [$t(22) = 0.72$, $p < .05$). From PV to PD, however, limb visible trials exhibited lower spatial correlations than limb occluded trials [t values (22) = 5.32 and 6.35, respectively, p values < 0.001) (Figure 3).

Discussion

Limb Vision and the Impact of a Stimulus Perturbation

Limb visible reaches were more accurate, slower, and spent more time in movement deceleration than limb occluded counterparts. Moreover, limb visible reaches elicited lower spatial correlations relating limb position at peak velocity and peak deceleration relative to ultimate movement endpoints (cf. Binsted & Heath, 2004, 2005; Heath, 2005; Heath et al., 2004b). These findings can be logically tied to the view that continuous limb vision permits the evocation of accurate and error-nullifying online limb corrections (Carlton, 1981; Meyer et al., 1988; Proteau, Marteniuk, & Levesque, 1992; Westwood, Heath, & Roy, 2001a; Westwood et al., 2003; Woodworth, 1899).

It is important to note that the majority of studies in the goal-directed reaching literature previously employing a perturbation technique have used a sudden and unexpected change in target location (e.g., Gentilucci, Chieffi, Scarpa, & Castiello, 1992; Goodale, Pelisson, & Prablanc, 1986; Heath, Hodges, Chua, & Elliott, 1998; Krigolson & Heath, 2006; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Soechting & Laquaniti, 1983). Indeed, perturbing the physical location of a target object mandates the use of online vision to implement movement corrections commensurate with new target position (i.e., the movement is controlled more online relative to reaches to a static target location).[3] Of course, the illusion-based perturbation used here provided that the addition of scene-based visual cues did not alter veridical movement endpoint. Given this treatment, the magnitude and timing of early and late reaching kinematics (i.e., PV, TPV, and TAPV) as well as movement duration (i.e., MT), endpoint accuracy and spatial correlations (i.e., R^2
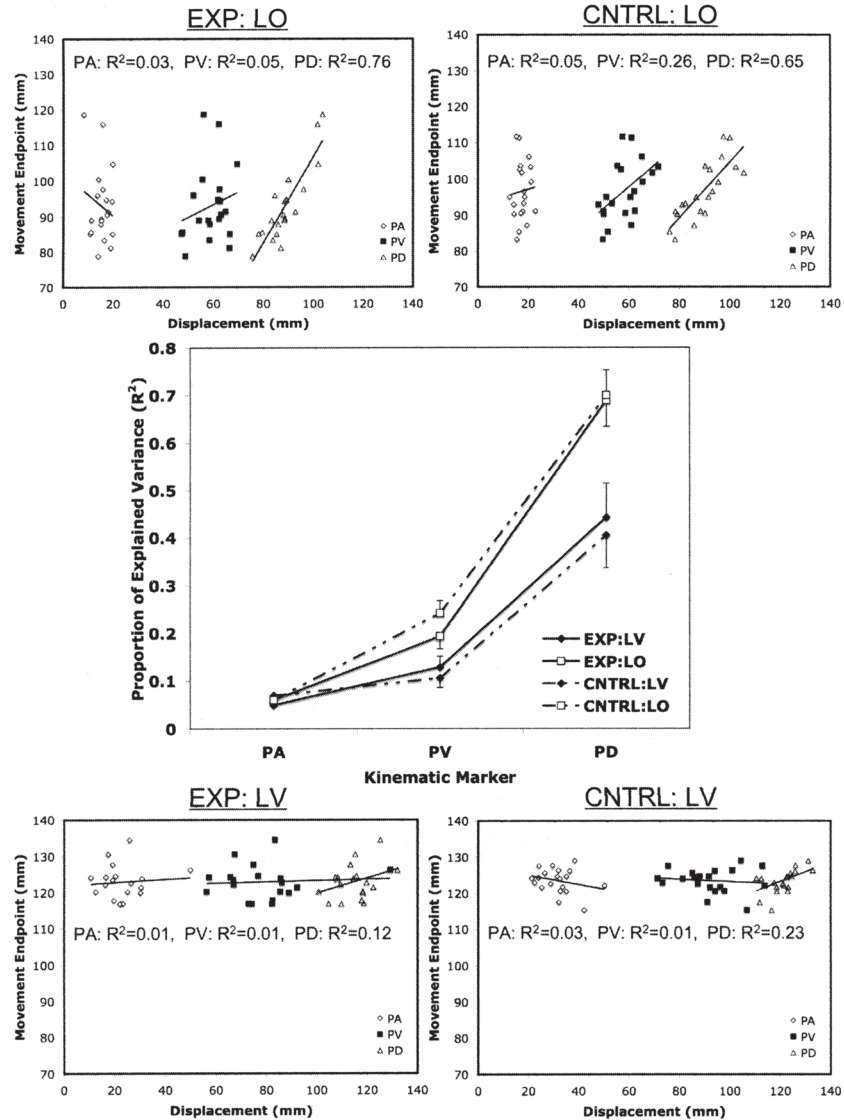
Figure 3—The center figure depicts mean proportion of variance (R^2) in movement endpoints explained by the position of the limb in the primary movement direction at three kinematic markers (PA = peak acceleration, PV = peak velocity, PD = peak deceleration) as a function of trial block (experimental, control) and limb condition (limb visible, limb occluded). Figures surrounding the main panel exhibit spatial correlations for an exemplar participant when reaching to the 9 cm control ML configuration. Note that regression lines and equations for the exemplar participant index the extent the spatial position of the limb at specific kinematic landmarks predicted ultimate movement endpoints.

values) did not vary as a function of experimental and control trials. Such a pattern indicates that our illusion-based perturbation did not alter the overall nature of reaching control.

The Nature of Visual Information Supporting Online Limb Adjustments

The magnitude of peak velocity as well as limb position at this kinematic marker did not scale in relation to the perceptual effects of the ML figures during experimental trials. The same metrics however, did scale in relation to the ML figures during control trials. Later in reaching movement (i.e., limb displacement at peak deceleration and movement endpoint) trajectory characteristics robustly scaled in a direction consistent with the perceptual effects of the ML figures for both experimental and control trials. That our experimental trials were selectively influenced by the ML figures late in the response is at odds with the PAM's notion that real-time control mechanisms residing in the visuomotor networks of the dorsal visual pathway process metrical object information for online limb adjustments (Westwood & Goodale, 2003; see Goodale, Westwood, & Milner, 2004 for recent review). As well, the present findings are not congruent with Glover's (2004) assertion that a context-independent "control representation" mediates online movement corrections.

Although the present findings differ from two extant models of visuomotor control, they are in accord with similar work employing an illusion-based perturbation (Handlovsky et al., 2004; Mendoza et al., 2006). Recall Mendoza et al.'s finding that introducing ML figures following movement onset had a biasing effect on the late kinematics of reaches performed with a contemporaneous saccadic response: a finding the authors interpreted to reflect the use of scene-based visual cues for online control. Of course, a goal of the present investigation was to determine whether Mendoza et al.'s findings were in part related to the purported biasing effects of saccadic drive on reaching control (e.g., Soechting et al., 2001). As such, participants in the present investigation maintained gaze on veridical movement endpoint in advance and during their reaching response. Interestingly, illusion effects associated with the perturbation trials in the present investigation (3.8 mm) parallel those reported by Mendoza et al. (see Experiment 1: illusion effects = 4.0 mm). Taken together, these results contend that biased saccadic drive does not impact the susceptibility of manual motor output to the ML figures (see also Bernardis, Knox, & Bruno, 2005).

An interesting result arising from our perturbation paradigm was the observation that illusion effects late in the reaching trajectory (i.e., PD and END) were greater for experimental than control trials. This result appears unrelated to the enhanced top-down or cognitive processing of visual context introduced to the reaching environment. Indeed, the fact that experimental trials elicited similar movement times and similar response strategies relative to control trials (see the section "Limb Vision and the Impact of an Illusion-Based Perturbation," above) indicates that allocentric visual cues were continuously integrated into the visuomotor system to implement online movement corrections. The heightened influence of the ML figures during perturbation trials may be best explained via the specialized role of

microsaccades in enhancing the spatial analysis of visual context (Bridgeman & Pacla, 1980). It is well known that experimental techniques calling for artificial stabilization of the retinal image engenders retinal image slip and diminished spatial analysis of scene-based information (see Ditchburn & Ginsborg, 1952). To counteract retinal slip, the visual system implements miniature eye movements (specifically microsaccades) to actively refresh static target information. More-over, a sudden change in visual display, such as the illusion-based perturbation used here, has been shown to amplify microsaccade frequency (Engbert & Kliegl, 2003) and the perception of peripheral stimuli (Martinez-Conde, Macknik, Tron-coso, & Dyar, 2006). We thus propose the enhanced effects of ML figures late in the trajectory of experimental trials is tied to increased microsaccade frequency and the associated integration of scene-based cues within the visuomotor system (Engbert & Mergenthaler, 2006).[4]

Concerning the impact of limb vision on the expression of illusion effects, some previous work has reported that online limb vision diminishes the biasing effects of the ML figures (de Grave et al., 2004; Gentilucci et al., 1996; but see Binsted & Elliott, 1999; Lavrysen et al., 2006). Gentilucci et al. interpreted this finding to reflect that continuous limb vision permits reaches to be specified pri-marily in an egocentric frame of reference, that is, with diminished influence from allocentric visual cues. Thus, one logical prediction for the present investigation asserts that reaches performed with limb vision would be largely refractory to the biasing effects of the ML figures due to their evocation of online and metrical limb/target corrections. A second prediction contends limb occluded trials would be impervious to an illusion-based perturbation because such actions are thought controlled without rigorous online limb adjustments (e.g., Carlton, 1981; Heath et al., 2004b; Meyer et al., 1988), thus limiting the opportunity for an "online" illusion to intrude into the unfolding trajectory. The present results, however, did not bear out the above predictions. Indeed, and in spite of the fact that limb visible reaches were controlled more online than limb occluded reaches (see the section "Limb Vision and the Impact of a Stimulus Perturbation," above), our results showed that visual feedback about limb position did not moderate the biasing effects of the ML figures. Moreover, the introduction of illusory structure following move-ment onset influenced the trajectories of limb occluded trials. In both cases such findings can only be tied to the integration of allocentric cues for online trajectory modification, or modifications.

In terms of reconciling the lack of support for the predictions outlined above, we propose that unitary and context-dependent visual information was used to support online reaching control regardless of the availability of continuous limb information (Franz, 2003). In support of this view, limb occluded trials performed with a concurrent illusion-based perturbation exhibited comparable illusion effects relative to trials performed with limb vision. In other words, aggregation of egocen-tric and allocentric visual cues was invariant to the degree reaches were controlled online. Such a proposal is congruent with findings showing that reaches performed with or without limb vision are similarly influenced by ML figures (e.g., Binsted & Elliott, 1999; Lavrysen et al., 2006). Moreover, converging evidence suggests geometric structure—apart from illusory arrays—surrounding a target object enhances the accuracy and stability of reaches performed with or without (e.g., Conti & Beaubaton, 1980; Krigolson & Heath, 2004; Redon & Hay, 2005; Velay

& Beaubaton, 1986) continuous limb vision. Thus, the present results contend that the availability of ego-motion signals (i.e., the moving limb) does not impact the nature of the visual information supporting the representation of a target object in peripersonal space.

Conclusions

Participants' online reaching control was reliably influenced by the illusion-evoking properties of the ML figures. Moreover, the biasing effects of the ML figures did not vary across the limb visible or limb occluded trials studied here. These findings are not in line with the view that online movement corrections are tied to the use of metrical visual information specified in an egocentric frame of reference (see Goodale et al., 2004 and Glover, 2004). Instead, the present results provide evidence for the emergent view that unitary visual information, combining egocentric and allocentric visual cues, supports the online control of action.

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Endnotes

1. Extensive behavioral and neuroimaging research has shown that reaches to a visible versus remembered target are supported via functionally and anatomically distinct cortical regions (for review, see Goodale et al. 2004). Because reaches in the present investigation were executed to a visible target we elected to contain our discussion to work involving actions directed to a continuously visible target object.

2. We also computed constant error (CE) in the primary movement direction. This analysis showed that limb occluded trials undershot target location more than limb visible trials, $F(1, 22) = 23.23$, $p < .001$, and that undershooting increased with increasing target length, $F(1, 22) = 14.18$, $p < .01$. Last, an effect for illusion, $F(2, 44) = 57.64$, $p < .001$, indicated that fins-in figures produced more undershooting than control figures [$t(22) = 4.91$, $p < .001$], in turn control figures elicited more undershooting than the fins-out figures [$t(22) = 6.92$, $p < .001$].

3. Research involving the double-step paradigm (e.g., Goodale et al., 1986) as well as studies employing an explicit and salient target perturbation (e.g., Heath et al., 1998) has shown that participants are able to rapidly and accurately use visual information to adapt to new target characteristics.

4. The eye-tracking technique used here was sensitive only to the detection of overt saccadic responses. Hence, it is important for the reader to bear in mind that our technique was not able to identify small amplitude saccades.