Title: Does the “eyes lead the hand” principle apply to reach-to-grasp movements evoked by unexpected balance perturbation?

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ABSTRACT

A fundamental principle that has emerged from studies of natural gaze behavior is that goal-directed arm movements are typically guided by a saccade to the target. In this study, we evaluated a hypothesis that this principle does not apply to rapid reach-to-grasp movements evoked by sudden unexpected balance perturbation. These perturbations involved forward translation of a large (2x6m) motion platform configured to simulate a “real-life” environment. Subjects performed a common “daily-life” visuo-cognitive task (find a telephone and make a call) that required walking to the end of the platform, which was triggered to move as they approached a handrail mounted alongside the travel path. A deception was used to ensure that the perturbation was truly unexpected. Eleven of 18 healthy young-adult subjects (age 22-30) reached to grasp or touch the rail in response to the balance perturbation. In support of the hypothesis, none of these arm reactions was guided by concurrent visual fixation of the handrail. Seven of the 11 looked at the rail upon first entering the environment, and hence may have used “stored” central-field information about the handrail location to guide the subsequent arm reaction. However, the other four subjects never looked directly at the rail, indicating a complete reliance on peripheral vision. These findings add to previous evidence of distinctions in the CNS control of volitional and perturbation-evoked arm movements. Future studies will determine whether similar visuo-motor behavior occurs when the available handhold is smaller or when subjects are not engaged in a concurrent visuo-cognitive task.

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1. INTRODUCTION

A fundamental principle that has emerged from studies of natural (unconstrained) gaze behavior is that “the eyes lead the hand” during volitional goal-directed arm movements. This is typically the case whether the arm movement is performed as an isolated aim, point, reach or reach-to-grasp task or occurs within the context of a more complex daily-life activity, and appears to apply for both rapid and preferred-speed movements (Abrams, 1992; Abrams et al., 1990; Carnahan & Marteniuk, 1991; Desmurget et al., 1998; Haycoe & Ballard, 2005; Land, 2006; Prablanc et al., 1979; Sivak & Mackenzie, 1992).

Typically, a saccade to the target is initiated prior to the start of the limb movement, although the limb may sometimes start to move first (Abrams, 1992). Nonetheless, because the saccade is much faster than the limb movement, visual fixation of the target almost always occurs well before the hand reaches the target (Abrams, 1992; Carnahan & Marteniuk, 1991). This gaze behavior facilitates control of the limb movement in two ways, by providing: (1) high-acuity retinal information about the location and characteristics of the target, as well as the relative position of hand and target during the final stages of the movement (Abrams, 1992); and (2) extra-retinal (oculomotor) information about the eye orientation and saccade amplitude that can also contribute to the programming of the limb movement (Enright, 1995; van Donkelaar, 1998).

Although it seems clear that “the eyes lead the hand” principle applies to a wide range of volitional motor behavior, the extent to which it governs the control of rapid reach-to-grasp movements evoked by sudden unexpected balance perturbation has not been established. These perturbation-evoked reactions are a prevalent response to sudden loss of balance, and can play an important role in preventing falls (Bateni et al., 2004; Maki & McIlroy, 1997; Maki & McIlroy, 2005; Maki et al., 1998; McIlroy & Maki, 1995b). The kinematic and electromyographic
features of these arm reactions are similar, in many respects, to volitional reaction-time reach-to-grasp movements elicited by a visual cue; however, the perturbation-evoked movements are typically initiated and executed much more rapidly than the fastest efforts to move the arm volitionally (Gage et al., 2007; Maki & McIlroy, 1997). For example, one balance-perturbation study reported a mean deltoid activation latency of 137ms, in comparison to 239ms for reactions elicited by a visual cue (subjects instructed to grasp a handrail as quickly as possible) (Gage et al., 2007), and other studies have reported mean perturbation-trial latencies as short as 90ms (McIlroy & Maki, 1995b). These latencies are very similar to the timing of the earliest lower-limb muscle activation (typically, 90-140ms at the ankle) that is evoked by balance perturbation (for reviews, see (Dietz, 1992; Horak & MacPherson, 1996; Maki & McIlroy, 2005)).

The urgent need to respond rapidly in order to maintain balance and prevent falling imposes temporal constraints that could possibly preclude the use of eye movements to guide the initial trajectory of perturbation-evoked reach-to-grasp movements. Typically, the time required to initiate a saccade is about 200ms (Trottier & Pratt, 2005) or longer (e.g. 300-500ms (Carnahan & Marteniuk, 1991)); however, this can be reduced to 90-120ms when there is a temporal gap between the offset of the initial fixation object and the onset of the peripheral target (Bekkering et al., 1996; Fischer & Ramsperger, 1984; Fischer & Weber, 1993; Trottier & Pratt, 2005). Although it is unclear whether these “express” or “gap-effect” saccades occur during natural behavior, it can be safely assumed that saccade initiation will require at least 90ms, and that the execution of the eye movement will require an additional 40-70ms (Pratt et al., 2006). Furthermore, the need to scan the environment to identify a suitable object to grasp could require multiple saccades, and the time required to process the visual information, after each saccade, would add further delays of 50ms or more per saccade (Findlay et al., 2001). These temporal considerations have led to the suggestion that the central nervous system (CNS) may avoid the
need to execute such saccades “online” (i.e. after perturbation onset) by instead utilizing visuo-
spatial information (VSI) that is either stored in memory or acquired online from the peripheral
visual field (Ghafouri et al., 2004). However, to our knowledge, the natural (unconstrained) gaze
behavior that actually occurs in reacting to an unexpected balance perturbation has not yet been
studied.

The present study is the first in a planned series of studies aimed at understanding the
visual control of rapid reach-to-grasp reactions evoked under conditions designed to simulate
“real-life” loss-of-balance situations, where the perturbation typically occurs suddenly and
unexpectedly. In these experiments, the perturbations are delivered via forward translation of a
large motion platform on which the subjects ambulate, and are triggered during the single-
support phase of the gait cycle so as to create a slip-like perturbation. To simulate a “real-life”
situation, the platform is configured to resemble a visually-complex office environment, and
subjects are asked to perform a typical task of daily life that requires walking to the end of the
platform. The platform translation is triggered to occur as the subject walks alongside a handrail
mounted on the platform, and a deception is employed to ensure that the perturbation is truly
unexpected. Analysis is restricted to one trial per subject - the subject’s first exposure to the
environment and perturbation. Although this single-trial approach severely limits the quantity of
data that can be collected, it is essential in order to avoid the adaptations that can occur when
multiple trials are performed (Maki & Whitelaw, 1993; McIlroy & Maki, 1995a; Oude Nijhuis et
al., 2009) or subjects know in advance that they may experience a balance perturbation (Pavol et
al., 2004).

The specific purpose of this initial study was to determine whether there is any evidence
that the “eyes lead the hand” principle applies to rapid reach-to-grasp reactions evoked by
unexpected balance perturbations, in healthy young adults. We hypothesized that this principle
would not apply, i.e. reach-to-grasp reactions would not be guided by a concurrent saccade to the handrail. Instead, we expected that the CNS would utilize stored VSI to guide the arm motion, acquired and stored upon entering the unfamiliar environment via natural exploratory gaze behavior (i.e. one or more saccades to the rail). A new methodology, developed by the authors (Scovil et al., 2009), was used in processing the gaze data in order to quantify the extent to which the rail was visible within the central and peripheral visual fields. A subset of the present data was included in a separate study addressing age-related changes in gaze behavior (King et al., 2009).
2. METHODS

2.1 Participants

The study involved ten male and eight female healthy young adults, with a mean age of 25 years (range 22-30), mean height of 173cm (range 154-189cm) and mean body mass of 73kg (range 48-127kg). All participants were naïve to the specific purpose of the study, and had not participated in any previous balance studies. All were right-handed, had a minimum corrected Snellen visual acuity of 20/40, and reported no neurological, sensory or musculoskeletal deficits. Each subject provided written informed consent, in compliance with the ethical approval granted by the institutional ethics review board.

2.2 Protocol

A large computer-controlled motor-driven motion platform (2x6m) was set up to simulate a “real-life” office environment, including a stair, handrail, desk and telephone, plus various visual distracters (Figure 1a, 1b). A wall and door prevented the subject from viewing the environment prior to the start of the trial. A standardized script informed the subjects that there was a room behind the door, with an office area located at the far end of the room, and instructed them to open the door, enter the room, walk to the end at a normal pace and make a telephone call. This task thus required performing a visual search for the telephone while walking to the end of the platform. For safety, all subjects wore a harness attached to a low-friction overhead track that moved smoothly and did not impede the subject’s movements.

--- insert Figure 1 about here ---

The handrail and stair were mounted near the middle of the platform (near-end of rail 1.8m from doorway, 1.5m in front of stair riser). Sudden forward translation of the platform (square-wave acceleration/deceleration profile: amplitude 3.5m/s², peak velocity 1.1m/s, displacement 0.43m, duration 0.6s) was triggered to occur when the subject stepped on a
pressure-sensitive mat adjacent to the handrail, thereby inducing a backward falling motion (similar to the effect of a slip). Objects mounted on the platform forced subjects to walk within a relatively narrow corridor (0.74m wide) when approaching the stair, and thereby ensured that the handrail was well within reach when the perturbation was delivered. The rail was cylindrical, with a diameter (38mm) and height (0.88m above leading edge of stair tread) previously shown to allow effective grasping by persons encompassing a wide range of body heights and hand sizes (Maki et al., 2006).

To avoid confounding effects of learning and adaptation, analysis was restricted to one trial per subject, which was the subject’s first exposure to the platform motion and to the simulated office environment. A deception was used to ensure that the perturbation was truly unexpected: subjects were told that the first trial was a “practice trial” to help them become accustomed to the testing procedure and that the platform would not move during this trial. The effectiveness of the deception was confirmed by querying the subjects after the trial, at which point the reason for the deception was explained.

Subjects were given no instructions regarding their gaze behavior.

2.3 Data collection and analysis

A lightweight head-mounted eye tracker (Model 501, Applied Sciences Laboratories, Bedford, MA, USA) was used to record eye movements (horizontal and vertical) at a sampling rate of 60 Hz. The tracker uses an infrared light source to produce a corneal reflection, which is detected, along with an image of the pupil, by a miniature video camera, and the separation between the corneal reflection and pupil is used to compute the angle of the line-of-gaze relative to the head. This is then used to determine the point-of-gaze location in relation to the video images recorded (at 60 Hz) by a miniature forward-facing “scene camera” (also mounted rigidly on the head), and the point-of-gaze is displayed as a cursor on these video images. Effects of
camera-lens distortion and other non-linearities are corrected by performing a calibration prior to the start of the experiment (ASL, 2000).

Custom-designed software (Scovil et al., 2009) was used to augment these point-of-gaze data by superimposing “gaze ellipses” (corresponding to visual angles of $5^\circ$, $10^\circ$, $15^\circ$, $20^\circ$, $30^\circ$ and $40^\circ$, in relation to the point-of-gaze) on each frame of the scene-camera video (Figure 1c). These images were used to determine whether visual fixation of the handrail occurred, as well as the onset time and duration of each such fixation or near-fixation. A fixation was defined to occur if the eye-tracker images showed that the point-of-gaze was stable (within $\pm2^\circ$) for $\geq100$ms, as per previous studies (Chapman & Hollands, 2010; Hollands et al., 2002; King et al., 2009; Panchuk & Vickers, 2006; Panchuk & Vickers, 2009; Patla & Vickers, 1997; Patla & Vickers, 2003; Vickers, 1996; Vickers & Williams, 2007). Handrail fixation was defined to occur if the fixation point-of-gaze was within $5^\circ$ of some portion of the handrail. For all other fixations, we characterized the proximity of the point-of-gaze to the rail in terms of the nearest gaze-ellipse annulus ($5-10^\circ$, $10-15^\circ$, $15-20^\circ$, $20-30^\circ$ or $>30^\circ$) that overlapped with some portion of the rail.

A three-dimensional video-based motion-analysis system (Vicon-Peak Performance, Oxford, UK) was used to characterize gross motor behaviors (opening of the hand aperture, grasping or touching the rail, overt reaching errors, compensatory step reactions, falls into the safety harness) and to determine: 1) time of initial rail contact; 2) time of grasp completion (all fingers wrapped around rail); 3) the trajectory of the reaching motion; and 4) turning of the head toward the rail. The system comprised four cameras that provided a calibrated viewing volume (~2m high, 2m wide, 3m long), centered near the near-end of the handrail. Coordinates of reflective markers placed bilaterally on the wrist (radial styloid), shoulder (acromion) and head (temples), as well as on the handrail, were digitized (60Hz) and low-pass filtered (6Hz cut-off).
The kinematic features of the arm reactions were characterized in terms of the motion of each wrist marker in relation to the ipsilateral shoulder marker. Motion of the right wrist marker in relation to the handrail markers was also used to characterize reaching responses. Transverse-plane head rotation (yaw), relative to the rail, was based on the angle of the line segment connecting markers on the left and right temples. Overt motor errors were defined to occur if there was a collision between the back of the hand and the handrail, or if the hand overshot the rail. Identification of hand-aperture opening was facilitated by reflective tape placed on the nail of the thumb and index finger. Arm-reaction onset-timing was derived from surface electromyographic (EMG) recordings from the right medial-deltoid and biceps-brachii (band-pass filtered, 10-500Hz; sampled at 1000Hz). EMG onset was determined by a computer algorithm (McIlroy & Maki, 1993) and confirmed by visual inspection. All EMG, kinematic and gaze timing values were defined relative to perturbation onset (PO) as recorded by an accelerometer (PO = platform acceleration >0.1m/s^2).
3. RESULTS

The main features of the arm reactions and associated gaze behavior are summarized in Table 1. Recorded data (yaw eye rotation relative to the head, yaw rotation of the head, lateral wrist displacement relative to the handrail, medial-deltoid EMG) for example trials are plotted in Figure 2, along with eye-tracker video-images showing the point-of-gaze at the onset of each new visual fixation. Key kinematic features of the arm movements are summarized in Figure 3, and example left and right arm trajectories (wrist relative to shoulder) are plotted in Figure 4. The timing of all visual fixations of the handrail (within a visual angle of 5°) is displayed, for each of the subjects, in Figure 5. The eye- and head-angle plots in Figure 2 are provided to illustrate the relative contributions of both eye and head rotations in achieving visual fixations; however, it is important to note that the fixations were also influenced by ongoing translation of the trunk and head. It is for this reason that stable fixations were defined on the basis of the eye-tracker video images, as detailed earlier in the Methods.

As detailed in Table 1, 11 of the 18 subjects grasped (n=6) or touched (n=5) the handrail with the right hand in reaction to the platform perturbation. Although all 11 ultimately grasped or touched the rail successfully, four made overt errors during the reaching motion. In one case, the back of the hand collided with the rail, and overshoot error (and subsequent reversal in wrist trajectory) was evident in three cases (e.g. see wrist displacement plot in Figure 2b).

--- insert Table 1 and Figure 2 about here ---

Of the seven subjects who did not grasp or touch the rail, three appeared to initiate a reach-to-grasp reaction (as evidenced by lateral displacement of the right hand toward the rail and opening of the right-hand aperture; Figure 4c) but did not contact the rail. The remaining four subjects moved both hands laterally but did not appear to reach for the rail, as evidenced by the absence of right-hand aperture opening (Figures 3b, 4b). They did, however, raise both arms
forward, consistent with a “counterbalancing” reaction that generates stabilizing reaction force/moment at the shoulders (Hoff, 2007). Additional stabilization was apparently provided via compensatory stepping, i.e. overt changes in the direction and/or step-length of the ongoing step (in progress at PO) and/or subsequent steps (Maki & McIlroy, 1997). All subjects took one or more compensatory steps (regardless of whether they used the handrail), and none fell or relied on the safety harness to prevent falling.

Typically, in both reach and non-reach trials, both arms tended to move forward, upward and laterally subsequent to PO; however, this was not always the case (e.g. small backward left-arm motion in subject S1, negligible vertical left-arm motion in S7; see Figure 3b). In addition, there was considerable variation in the spatial and temporal features of the arm movements (Figures 3b, 4). It seems likely that at least some of the variation may have been a consequence of the variability in the position and velocity of the arms at time of PO (Figure 3a).

--- insert Figures 3 and 4 about here ---

The tabulated and plotted gaze data (Table 1; Figures 2 and 5) clearly show that the arm movements were not guided by concurrent visual fixation of the handrail. Firstly, there was no evidence that any of the 11 subjects who grasped or touched the handrail were looking at the rail at time of perturbation onset (PO). Stable fixations at time of PO were identified in 10 of these 11 subjects, with gaze directed at the telephone (N=4), desk/computer (N=3), chair (N=2) or stair (N=1), and the visual angle from this gaze location to the nearest portion of the rail was >10° in each case. Moreover, although 10 of the 11 subjects executed a post-PO saccade prior to completing the grasp or touch of the rail, none of these saccades resulted in handrail fixation. Gaze was instead redirected at the chair (N=3), far handrail post (N=2), computer monitor (N=2), floor near the chair (N=1), stair (N=1) or telephone (N=1). Five subjects also made a second post-PO fixation prior to grasp/touch completion, fixating either the chair (N=2), floor (N=1),
desk (N=1) or telephone (N=1), and two subjects made a third post-PO fixation which was directed at the telephone. For all post-PO fixations, the visual angle from the fixation point-of-gaze to any portion of the handrail was never less than 5°, and the visual angle to the hand itself was never less than 15°. The probability that the observed gaze behavior (i.e. post-PO rail fixation in 0 of 11 subjects) would occur by chance alone is very small (p<0.001; exact binomial test); hence, these data strongly support our hypothesis that the reaching movement would not be guided by central visual fixation of the rail.

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The closest (most central) post-PO rail fixations occurred in the two subjects who made post-PO fixations of the handrail post (subjects S6 and S10, in Table 1). These fixations brought a portion of the rail within the central 10° of the visual field; however, they began well after the initiation of the arm reaction (>125ms after the earliest arm-muscle activation). In both cases, the timing of these relatively late fixations appeared to be more closely associated with an overshoot error and the subsequent corrective reversal in the wrist trajectory (e.g. Figure 2b).

Although there was no evidence of the “eyes leading the hand” during the execution of the arm reaction, seven of the 11 subjects who used the handrail did fixate on it (within a visual angle of 5°) one or more times after opening the door and entering the test environment, prior to PO. Hence, “stored” central-field information about the handrail was potentially available to aid in programming the perturbation-evoked arm reaction. The other four subjects (S1, S2, S7 and S8 in Table 1) never looked directly at the rail at any time prior to rail-contact (before or after PO), yet grasped or touched the rail without overt error (e.g. Figure 2a). The fact that the rail was never brought within the central 5° of the visual field indicates that these four subjects relied entirely on more peripheral regions of the visual field to locate the rail.

The seven subjects who did not contact the rail showed no obvious differences in gaze
behavior, in comparison to the 11 subjects who grasped or touched the rail. Gaze data were missing or incomplete for two of these seven subjects (due to technical problems); however, none of the remaining subjects fixated on the rail at or after PO. Conversely, all but one did fixate on the rail (within 5°) one or more times prior to PO.
4. DISCUSSION

The results of the study clearly support the hypothesis that reach-to-grasp reactions evoked by unexpected balance perturbation would not be guided by a concurrent visual fixation of the handrail. Indeed, none of the 11 subjects who grasped or touched the handrail in reaction to the perturbation executed a saccade to the rail in conjunction with the initiation of the reaching movement, and none were looking at the rail at time of perturbation onset (PO). There were no cases where a post-perturbation fixation brought the rail within the central 5° of the visual field, and only two cases where the visual angle to any portion of the rail was within 10°. The latter two fixations both began well after the initiation of the arm reaction, and appeared to be associated with the correction of an overshoot error. These findings demonstrate gaze behavior that is distinctly different from that observed during studies of unconstrained volitional goal-directed arm movements, and suggest that the “eyes lead the hand” principle that typically governs such volitional movements may not apply to compensatory arm movements evoked by unexpected loss of balance in typical daily-life situations and environments.

As detailed in the Introduction, the differing visual control strategies used in compensatory and volitional arm movements may arise as a consequence of the temporal constraints that govern perturbation reactions, i.e. the need to react very rapidly in order to prevent a fall. Another possibility is that the gaze behavior observed during the perturbation reactions was influenced by other task demands, such as the need to avoid tripping over objects in the course of recovering equilibrium. The reach-to-grasp reactions were always accompanied by compensatory stepping reactions, during which it has been shown that gaze is sometimes redirected downward toward the floor (Zettel et al., 2005; Zettel et al., 2008; Zettel et al., 2007). However, in the present study, gaze was redirected toward the floor or stair, subsequent to PO, in only three of the 11 trials that involved grasping or touching of the rail. More frequently (8 of 11
cases), subjects maintained or redirected gaze at objects related to the telephone task (i.e. the desk or objects mounted on the desk). This is consistent with previous findings that subjects are much less likely to look downward during stepping reactions when engaged in an ongoing visuo-cognitive task (Zettel et al., 2008). Potentially, failure to disengage attention from the telephone task in the present study could have also had an analogous effect in inhibiting redirection of gaze toward the handrail. Further work is needed to determine whether, in fact, subjects are more likely to look at the handrail during the perturbation-evoked reaction when there is no concurrent visuo-cognitive task.

The finding that online central-field fixation of the handrail did not occur implies that initial arm movement was instead guided using: 1) online VSI from the peripheral field, and/or 2) VSI acquired and stored during pre-PO fixations that captured the rail either centrally or peripherally. Although most subjects did fixate centrally on the rail one or more times prior to PO, the fact that four subjects grasped or touched the rail without ever fixating on it suggests that peripheral vision may play an important role in guiding these balance-recovery reactions, and adds to the balance literature indicating that peripheral vision can also contribute significantly to stabilizing the head and/or body (Bardy et al., 1999; Berencsi et al., 2005; Schmid et al., 2008). Studies of volitional reaching or pointing arm movements would indicate that the reliance on either stored target information (Heath & Binsted, 2007; Jackson et al., 1995; Kopinska & Harris, 2003; Lemay & Stelmach, 2005) or peripheral vision (Bock, 1986; Bock, 1993; Henriques & Crawford, 2002; Henriques et al., 1998; Lewald & Ehrenstein, 2000) will reduce the accuracy of the end-point control. Although the length of the handrail used in the present study allowed considerable leeway for error in terms of antero-posterior hand placement, the narrow width of the rail presented demands for lateral reach accuracy that are comparable to many previous volitional-reach studies, and the high frequency of reaching errors (4 of 11 trials)
speaks to the challenge of these accuracy demands. Further studies are needed to determine whether the gaze behavior associated with perturbation-evoked reactions is affected by the dimensions of the objects that are available to touch or grasp for support.

The pre- and post-PO gaze behavior of the seven subjects who did not use the handrail to aid in balance recovery appeared to be very similar to that of the 11 subjects who grasped or touched the rail. It is not clear why these seven did not use the rail to aid in balance recovery. The data provide no compelling evidence to suggest that a failure to “notice” the rail or to map its location was a factor, as there was only one case where the subject did not fixate on the rail prior to PO. For the three subjects who appeared to initiate a reach, undershoot error is a possible explanation for the failure to contact the rail, however, one would expect such error to be followed by attempts to correct the arm trajectory, and we observed no overt evidence of such corrective efforts. Rather, it appears more likely that these were aborted reach-to-grasp reactions, in which the reaction is initiated rapidly to safeguard against falling but is subsequently aborted (McIlroy & Maki, 1995b).

The present results were based on a 100-ms criterion for gaze fixation. This criterion has been commonly used in gaze-behavior studies (see citations in Methods), is based on minimum fixation durations observed during such studies (see (Vickers, 1996)), and presumably reflects the minimum time needed to acquire and process the required VSI. To examine the effect of using this fixation criterion, we repeated the analyses using a 50-ms criterion. Fixation times as short as 50ms occur rarely during visual-search tasks, even when subjects are well practised and search rapidly for a well-defined and highly-visible target (Findlay et al., 2001); therefore, it seems unlikely that fixation times as short as this would suffice in the present study, where the visual environment was unfamiliar and complex. However, even when using the 50-ms criterion, the main results were largely unchanged: 10 of 11 handrail users continued to exhibit
no evidence of central-field (0-5°) handrail fixation after PO (the remaining subject, S9, exhibited a 67ms fixation that began 135ms after the onset of the arm reaction), and all four subjects who were previously inferred to rely entirely on peripheral vision continued to show no rail fixations either before or after PO.

The present study is subject to a number of limitations. First, the single-trial/deception paradigm that was used to prevent adaptation limited the study to a relatively small set of observations. Although the current sample was sufficient to provide statistical support for our central hypothesis, it is clear that larger numbers of subjects will need to be tested in order to obtain reliable estimates of the incidence rate for specific observed behaviors, e.g. reaches that are guided entirely by peripheral vision. Another limitation is that our focus on natural behavior allowed wide variation in visual inputs (e.g. timing and duration of central-field rail fixation) and limited control over kinematic variables such as gait speed, posture and position/motion of the body/limbs in relation to the handrail at PO. Thus, although the current approach is valuable in revealing natural behavior, there is a need for complementary studies that probe the control mechanisms and mediating factors by manipulating and/or controlling specific visual and kinematic variables. For example, partially-occluded contact lenses can be used to force reliance on peripheral or central vision (Sivak & MacKenzie, 1990; Sivak & Mackenzie, 1992), and liquid-crystal goggles can force reliance on stored or online VSI (Cheng et al., 2009a; Scovil et al., 2008). Control over initial kinematic conditions can be achieved by applying perturbations to stationary subjects, while using motor-driven devices to introduce well-controlled variation in the location of surrounding obstacles or handholds (Cheng et al., 2009b; Scovil et al., 2008; Zettel et al., 2007).
5. CONCLUSION

The results presented here demonstrate that the initiation of reach-to-grasp reactions evoked by unexpected balance perturbation was not guided by concurrent central-field visual fixation of the grasp target. Hence, one must conclude that the initial arm movement was instead guided using stored central-field VSI, stored peripheral-field VSI and/or online peripheral-field VSI, and further work is needed to determine the degree to which these alternate sources of VSI are necessary or sufficient. Although the “eyes lead the hand” principle that has emerged from studies of volitional arm movements clearly did not govern the reactions evoked in the present study, it remains to be determined whether this principle applies when the target handhold is smaller or when there is no concurrent visuo-cognitive task. Nonetheless, the present findings add to the literature indicating possible distinctions in the CNS control of volitional and compensatory arm movements, and point to the importance of considering these distinctions during the clinical assessment and treatment of movement and balance deficits.
6. ACKNOWLEDGMENTS

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7. REFERENCES


8. TABLE (see attached file)

9. FIGURE CAPTIONS

Figure 1: Methodological details. A. Schematic drawing of the large (2mx6m) motion platform used to evoke the reach-to-grasp reactions. B. Photograph showing the view seen by the subject after opening the door at the start of the trial (the telephone that the subject was instructed to find is located on the desk, next to the computer monitor). C. Example eye-tracker scene-camera video-image, showing the point-of-gaze cursor and the “gaze ellipses” corresponding to visual angles of 5°, 10°, 15°, 20° and 30° (in the displayed image, gaze is fixated on the computer monitor and the far end of the handrail is visible within a 15° visual angle). Adapted from (King et al., 2009; Maki et al., 2008; Maki & McIlroy, 2007; Scovil et al., 2007).

Figure 2: Recorded data for example trials. A shows an error-free grasp reaction (subject S1 in Table 1), while B depicts an overshoot error during which the thumb contacted the rail (subject S6). Each panel displays horizontal (yaw) eye rotation (relative to the head), transverse-plane (yaw) head rotation, lateral displacement of the right wrist marker (relative to the handrail) and rectified EMG (right medial-deltoid). Downward displacements indicate lateral (rightward) motion. The vertical lines indicate time of perturbation onset (PO), onset of deltoid activation (DO), initial contact with the rail (IC), grasp completion (GC), and the onset of each visual fixation occurring after PO (F2, F3). The broken horizontal line indicates the location of the handrail in relation to the wrist marker. The inset images from the eye-tracker scene-camera show the point-of-gaze (black dot within a white circle) at the onset of the indicated post-PO visual fixations (F2, F3), as well as the fixation in effect at time of PO (F1); the black ellipses indicate visual angles of 5°, 10°, 15°, 20° and 30° with respect to the point-of-gaze. These images clearly indicate that the arm reaction was initiated in the absence of any direct fixation of
the handrail (i.e. visual angle always >5°). Although there was an early post-PO saccade in A (F2), the fixation onset began ~50ms after the initiation of the arm reaction in deltoid (DO) and >150ms after biceps activation (see Table 1). Furthermore, this saccade did not result in central fixation of the rail (visual angle >20°). A more central fixation (5-10°) did occur in B (F2), but this was much later in the response, after initial contact with the handrail and during the overshoot correction (i.e. the reversal in the direction of the wrist motion). For this reason, A is adapted from (King et al., 2009).

**Figure 3:** Key kinematic features of the arm reactions: A. position and velocity of each arm at time of perturbation onset (PO); B. maximum displacement and velocity of each arm during the response to the perturbation. Gray and black bars correspond to the left and right arms, respectively. The displayed data represent the motion of the wrist marker relative to the ipsilateral shoulder marker. The data in B represent the maximum values that occurred along the antero-posterior, medio-lateral and vertical axes during the initial arm movement evoked by the perturbation (i.e. prior to any reversal in direction), within 1.0s of PO. Positive values (to the right of the vertical zero-line) indicate motion in the forward, lateral or upward direction; zero displacement indicates a position where the wrist marker is directly below the shoulder marker, with the arm fully extended. To facilitate comparison between subjects, displacements and velocities are scaled as a percentage of subject height, as per the indicated scaling bars (note the different scaling in A and B). The numerical values listed to the left of each bar, in B, indicate the time (in ms) at which the maximum displacement or velocity occurred, relative to time of PO.

**Figure 4:** Example right (solid line) and left (broken line) arm trajectories for trials involving: A. a reach-to-grasp reaction (subject S4), and B. a reaction that did not appear to involve reaching for the rail (subject S16) and C. an apparent reach reaction that did not result in handrail contact.
(subject S14). Each plot shows the displacement of the wrist marker in relation to the ipsilateral shoulder marker. Upward displacements on the graphs indicate forward, rightward or upward wrist motion. The vertical lines indicate time of perturbation onset (PO), time of initial rail contact (IC), time of grasp completion (GC), and the time corresponding to the displayed video images (VI). Each plot displays 1.1s of data (0.1s prior to PO, 1.0s after PO). The accompanying video images display the arm displacement at time of maximum lateral right-wrist displacement, and illustrate the opening of the hand aperture that occurred during reach reactions (A and C) and the absence of aperture opening that appears to indicate the absence of an effort to reach for the rail (B) [white circles have been drawn to highlight the location of reflective tape placed on the nail of the right thumb and index finger].

**Figure 5:** Visual fixation of the handrail displayed as a function of time, for each of the subjects. Time-zero corresponds to the onset of the balance perturbation (platform acceleration >0.1m/s²); negative and positive time values (in seconds) correspond to events occurring before and after perturbation onset (PO), respectively. Each darkened portion of each bar represents an interval during which gaze was fixated on the handrail (within a visual angle of 5°). The gray vertical line segments superimposed on the bars indicate the time at which initial contact with the rail occurred, in grasp and touch trials. In addition, for grasp trials, the black vertical line segments indicate the time at which the grasp was completed (fingers fully wrapped around the rail). Note that none of the subjects fixated on the handrail during the interval between PO and contact with the rail. Eleven subjects fixated on the rail one or more times prior to PO, while five subjects (four of whom grasped or touched the rail) never fixated on the rail at any time (before or after PO). Note: due to technical problems, S3 had no gaze data prior to the pre-PO fixation marked with the *, S18 had no gaze data during the post-PO interval, and S14 had no gaze data for the entire trial.
Table 1: Summary of the perturbation-evoked arm reactions and associated gaze behavior [central fixations of the handrail (i.e. rail within 5° of the point-of-gaze) are highlighted in bold text]

<table>
<thead>
<tr>
<th>Subject</th>
<th>Arm reactions</th>
<th>Gaze fixations$^9$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Overt error</td>
<td>Timing (ms)$^1$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>EMG onset Deltoid</td>
</tr>
<tr>
<td>S2</td>
<td>---</td>
<td>195 189 708 775</td>
</tr>
<tr>
<td>S3</td>
<td>---</td>
<td>217 227 613 780</td>
</tr>
<tr>
<td>S4</td>
<td>---</td>
<td>176 189 612 728</td>
</tr>
<tr>
<td>S5</td>
<td>collision</td>
<td>206 207 417 883</td>
</tr>
<tr>
<td>S6</td>
<td>overshoot</td>
<td>185 n/a 465 998</td>
</tr>
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</table>

TOUCH OF RAIL (but no prehension):

<table>
<thead>
<tr>
<th>Subject</th>
<th>Arm reactions</th>
<th>Gaze fixations$^9$</th>
</tr>
</thead>
<tbody>
<tr>
<td>S7</td>
<td>---</td>
<td>259 234 672 ---</td>
</tr>
<tr>
<td>S8</td>
<td>---</td>
<td>288 222 747 ---</td>
</tr>
<tr>
<td>S9</td>
<td>---</td>
<td>117 168 652 ---</td>
</tr>
<tr>
<td>S10</td>
<td>overshoot</td>
<td>202 155 598 ---</td>
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</tbody>
</table>

REACH TOWARD RAIL (but no rail contact):

<table>
<thead>
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<th>Subject</th>
<th>Arm reactions</th>
<th>Gaze fixations$^9$</th>
</tr>
</thead>
<tbody>
<tr>
<td>S12</td>
<td>---</td>
<td>rail 0-5° -483</td>
</tr>
<tr>
<td>S13</td>
<td>---</td>
<td>post 0-5° -3142</td>
</tr>
<tr>
<td>S14</td>
<td>---</td>
<td>249 203 --- ---</td>
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</table>

NO OVERT REACH TOWARD RAIL:

<table>
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<th>Arm reactions</th>
<th>Gaze fixations$^9$</th>
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<tbody>
<tr>
<td>S15</td>
<td>---</td>
<td>rail 0-5° -310</td>
</tr>
<tr>
<td>S16</td>
<td>---</td>
<td>post 0-5° -3448</td>
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<tr>
<td>S17</td>
<td>---</td>
<td>rail 0-5° -3880</td>
</tr>
<tr>
<td>S18</td>
<td>---</td>
<td>stair 20-30° -548</td>
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</tbody>
</table>

$^9$ See Figure 1b for a photograph showing the location of the various fixation targets noted in the table ("post" indicates the vertical post supporting the far end of the handrail; "monitor" indicates the computer monitor located on the desk).

$^1$ All timing values are in relation to perturbation onset (time=0.0); negative values indicate events occurring prior to perturbation onset.

$^2$ For the pre-perturbation fixations, the listed gaze data correspond to the nearest fixation (smallest visual angle) with respect to the handrail.

$^3$ For the fixations occurring after perturbation onset, only fixations beginning prior to touch or grasp completion are listed, in grasp/touch trials. For the other trials, all fixations beginning within 1s of perturbation onset are listed.

$^6$ No stable fixation.

Data not available due to technical problems.
Figure(s)
<table>
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<tr>
<th></th>
<th>Displacement</th>
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<tr>
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<td>S1</td>
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<tr>
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</tr>
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</tr>
<tr>
<td>S13</td>
<td></td>
<td></td>
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<td>S14</td>
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<tr>
<td>No overt reach toward rail</td>
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<tr>
<td>S15</td>
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<tr>
<td>S16</td>
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<tr>
<td>S18</td>
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Legend:
- **Left**
- **Right**

10% of body height

25% of body height per second