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RESEARCH ARTICLE

Effects of roll visual motion on online control of arm movement: reaching within a dynamic virtual environment

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Abstract Reaching toward a visual target involves the transformation of visual information into appropriate motor commands. Complex movements often occur either while we are moving or when objects in the world move around us, thus changing the spatial relationship between our hand and the space in which we plan to reach. This study investigated whether rotation of a wide field-of-view immersive scene produced by a virtual environment affected online visuomotor control during a double-step reaching task. A total of 20 seated healthy subjects reached for a visual target that remained stationary in space or unpredictably shifted to a second position (either to the right or left of its initial position) with different inter-stimulus intervals. Eleven subjects completed two experiments which were similar except for the duration of the target's appearance. The final target was either visible throughout the entire trial or only for a period of 200 ms. Movements were performed under two visual field conditions: the virtual scene was matched to the subject's head motion or rolled about the line of sight counterclockwise at 130°/s. Nine additional subjects completed a third experiment in which the direction of the rolling scene was manipulated (i.e., clockwise and counterclockwise). Our results showed that while all subjects were able to modify their hand trajectory in response to the target shift with both visual scenes, some of the double-step movements contained a pause prior to modifying trajectory direction. Furthermore, our findings indicated that both the timing and kinematic adjustments of the reach were affected by roll motion of the scene. Both planning and execution of the reach were affected by roll motion. Changes in proportion of trajectory types, and significantly longer pauses that occurred during the reach in the presence of roll motion suggest that background roll motion mainly interfered with the ability to update the visuomotor response to the target displacement. Furthermore, the reaching movement was affected differentially by the direction of roll motion. Subjects demonstrated a stronger effect of visual motion on movements taking place in the direction of visual roll (e.g., leftward movements during counterclockwise roll). Further investigation of the hand path revealed significant changes during roll motion for both the area and shape of the 95% tolerance ellipses that were constructed from the hand position following the main movement termination. These changes corresponded with a hand drift that would suggest that subjects were relying more on proprioceptive information to estimate the arm position in space during roll motion of the visual field. We conclude that both the spatial and temporal kinematics of the reach movement were affected by the motion of the visual field, suggesting interference with the ability to simultaneously process two consecutive stimuli.

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Introduction

In daily life, reaching toward objects often occurs during complex movements of our body and of the physical world. Hence, the spatial relationship between our hand and the space in which we plan to reach may vary at any time. To reach for a target accurately, the central nervous system uses a series of computational processes that take into account both the target's position and the arm's initial position (Flash and Sejnowski 2001). Further, body posture and arm movement must also be coordinated (Massion et al. 2004). Such online control is particularly apt in overcoming external perturbations likely to impair movement accuracy.

It has been shown that visual information related to the spatial characteristics of the target plays a major role for the planning and online control of movement (e.g., Desmurget et al. 1998; Sarlegna et al. 2003). In the past few decades, the 'double-step target displacement' paradigm has been extensively used to study the contribution of target information to the online control of arm movements in both nonhuman primates (e.g., Georgopoulos et al. 1981) and humans (e.g., Desmurget et al. 1999; Dvorkin 2004; Farnè et al. 2003; Goodale et al. 1986; Henis and Flash 1995; Pisella et al. 2000; Prablanc and Martin 1992; Soechting and Lacquaniti 1983). According to this paradigm, the goal-target is unexpectedly displaced either before or following movement initiation or at movement onset. A successful reach toward the displaced target requires the subject to amend the planned motion after the initial preparation for the movement has commenced. Numerous studies have shown that nonhuman primates as well as both young and elderly healthy humans are able to modify their arm movements in response to the unexpected change in target position. Recently, Martin et al. (2003) investigated the efficiency of online visuomotor control of goal-directed arm movement while standing and viewing a stationary scene generated by a virtual environment (VE). Using the double-step reaching task, the authors demonstrated that online control processes of arm movement were preserved when performed in a VE provided that the environment remained stable.

An interesting observation to contrast with the previous double-step studies which used a stationary environment would be to explore functional arm movements taking place when the external world was moving at the same time as the arm. Subjects might then need to further modify their motor plan with regard to the external space. The visuomotor system can accomplish this by continuously updating internal representations using various available sources of information. For example, retinal motion information, and extra-retinal information such as proprioceptive information about limb position, efference copy of arm and eye movement commands, and vestibular information about body position (Brouwer et al. 2006; Henriques et al. 1998; Whitney and Goodale 2005). However, failures to perform well could arise from a variety of possible underlying processes. It has long been demonstrated that motion of the visual scene affects motor behavior, (postural control and reaching). Over the years, a wide variety of moving visual stimuli have been employed to study this issue such as tilting or rotating rooms or projected displays simulating a moving visual scene (e.g., Cohn et al. 2000; Streepey et al. 2007). Previous postural control studies have shown an increase in postural instability in a moving visual environment (Keshner and Kenyon 2004; Keshner et al. 2004; Mergner et al. 2005), with robust postural changes in the roll and pitch planes (Previc 1992). Previous reaching studies have shown different effects of visual motion on movement control processes (e.g., Gomi et al. 2006; Whitney et al. 2003, 2007; Whitney and Goodale 2005). For example, Saijo et al. (2005) reported a rapid manual response to follow a sudden movement of the visual background. Whitney et al. (2003) have shown that subjects shifted their hand in a direction consistent with the motion of a distant and unrelated stimulus, during fast reaching movements toward a briefly presented stationary target. They further reported that this occurred continuously from movement programming through to its execution. Finally, Lackner and DiZio have shown in a series of studies, an increase in errors when pointing to targets during whole-body rotation, while subjects sat in a rotating chamber. By contrast, they reported that pointing made during natural voluntary torso rotation seemed to be accurate (Cohn et al. 2000; Lackner and DiZio 1998). These authors argued that the inertial Coriolis forces generated by reaching movements in the rotating environment initially disrupted movement trajectory and endpoint (Lackner and DiZio 2005). Furthermore, these errors in movement paths and endpoints showed a mirror image pattern for rotation in the opposite direction (Cohn et al. 2000). Although the effects of visual motion on control of arm movement have been extensively investigated, much of the research on the subject has been carried out on simple point-to-point movements, thus, the exact role of visual motion in human motor control still remains unclear.

In the past decade, a growing number of studies have demonstrated the efficacy of using virtual reality technology in investigating arm movement control processes (Dvorkin et al. 2006; Kuhlen et al. 2000; Martin et al. 2003; Viau et al. 2004). One of the cardinal strengths of virtual reality technology is that it provides us the capability to easily and precisely manipulate the environment and virtual objects that appear within it (e.g., to simulate visual motion). To better understand the role of visual motion in online control of movements we have investigated the effects of roll visual motion, created within a VE, on planning and execution of simple and complex three-dimensional (3D) reaching movements, using the double-step task. Rotation of the visual display induced errors in reaching (Coello et al. 2004). Furthermore, roll visual motion was found to produce robust perceptual effects and postural changes (Brandt et al. 1973; Previc 1992). Since the localization of both the target and hand in space are derived from sensory information we expected to find the strongest effect on reaching during visual roll motion. Particularly, we assumed that roll motion of the visual environment might easily perturb performance on a complex movement task such as the double-step task.

In a previous study with a small number of subjects we have described preliminary observations on the effect of roll visual motion on reaching, where subjects were exposed to an immersive 3D VE which was either matched to their head motion or rolled counterclockwise for a short time at a constant velocity (Dvorkin et al. 2007). We have found that motion of the visual field mainly affected reaching toward a remembered target location. However, these data only partially supported the original hypothesis. The present study was designed to fully explore the intriguing findings from the preliminary study. Here, we further analyze the spatial and temporal kinematics of the movement of 11 subjects and provide robust quantitative evidence for the observed effects of roll motion on timing and kinematic adjustments of the reach. To test the hypothesis that roll visual motion might hinder the timing of reaching parameters and kinematic adjustments (updating processes), we compared trials from both scene conditions. Furthermore, to test our assumption that a visual target visible during the entire trial might reduce the observed effects of roll motion on performance, subjects were tested in a second experiment in which a final target appeared for only 200 ms in each trial. Finally, to examine the effect of manipulating the direction of visual roll motion on reaching, 9 new subjects completed a third experiment in which both clockwise and counterclockwise roll motions were used.

Experiments 1 and 2

Materials and methods

Subjects

Eleven young healthy adults (five males, six females; aged 24–36 years) participated in the study. All subjects were right-handed and had normal or corrected-to-normal vision. Subjects gave informed consent in accordance with the Institutional Review Board of Feinberg School of Medicine, Northwestern University.

Apparatus and data collection

Subjects were immersed in a 3D wide field-of-view VE (scene), which was projected via a stereo-capable projector (Electrohome Marquis 8500) onto a 2.6 m × 3.2 m back-projection screen. The projector throws a full-color stereo workstation field (1,024 × 768 stereo) at 120 Hz onto the screen. The environment consisted of a 30.5 m wide by 6.1 m high by 30.5 m deep room containing round columns with patterned rugs and painted ceiling. Beyond the virtual room was a landscape consisting of mountains, meadows, sky and clouds. Visual targets, which appeared in three possible locations with the scene, were generated as 3D virtual ball-shaped targets (Fig. 1a). Field sequential stereo images of the environment were separated into right and left eye images using liquid crystal stereo shutter glasses worn by the subject (Crystal Eyes, StereoGraphics Inc.). The shutter glasses limited the subject's horizontal field-of-view to 100° of binocular vision and 55° for the vertical field-of-view. Since the experiment room was dark with painted black walls and floor, the subject's immersion in the VE was not compromised by a peripheral stationary reference. The correct perspective and stereo projections for the scene were computed using values for the current orientation of the head (6 DOF) supplied at 120 Hz by reflective markers (Motion Analysis) attached to the stereo shutter glasses. Consequently, virtual objects retained their true perspective and position in space regardless of the subjects' movement (i.e., the scene was matched to the subject's head motion).

Reflective markers were attached bilaterally on the acromion process, lateral epicondyle of the humerus, styloid process of the ulna, second metacarpophalangeal joint, and zygomatic arch. Markers were also placed on the sternum, C7 and on L4/L5 joint of the spine. A six camera Motion Analysis system (Motion Analysis, Inc.) was used to capture joint motion at 120 Hz. Commercial software (EVaRT and Matlab) were used to generate and analyze the kinematic data of 3D arm movements.

Procedures

All subjects completed both Experiments 1 and 2; five subjects were exposed to Experiment 1 then Experiment 2 and six subject to the reverse order. The experiments were randomly presented to minimize order dependencies. Subjects sat comfortably on a stationary stool located at a fixed distance (1.2 m) from the screen, with their feet in full contact with the floor, and reached with their right arm

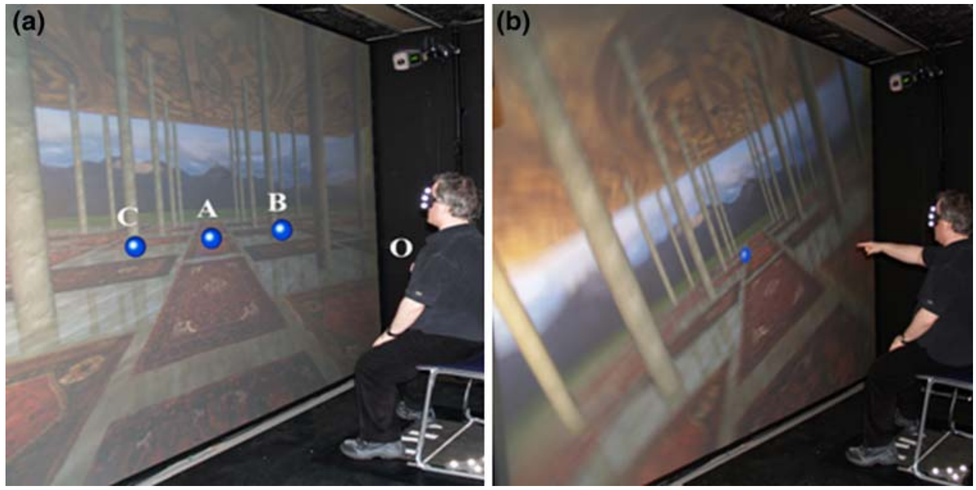

Fig. 1 **a** Spatial arrangement of visual targets. Note that the *letter* labels do not appear within the VE. **b** Screen shot of an individual performing during roll motion of the VE

toward virtual visual targets. Subjects could see their own moving arm. Three visual targets appeared within the VE as blue spheres with a 1 cm radius (defined as A, B and C in Fig. 1a). Sequence and duration of the targets' appearance was controlled. At the start of each experiment, spatial position of each target was defined in terms of the arm length and sternum position of the subject. The central target (A) was located directly in front of the subject at a distance equal to 90% of arm length and 20 cm above the sternum position. The other targets were located 15 cm to the right (B) or left (C) of the central target.

Experiment 1

Each experiment began with 20 practice trials. Five blocks of trials were presented, each containing 12 single-step trials (with configurations OA, OB and OC) and 24 double-step trials (with configurations OAB and OAC) in random order. A 2 min rest period was given between each block. For half of the trials in each block, subjects were exposed to a visual scene which was matched to head motion ('Still condition'). For the remaining half of the trials, the visual scene rotated in a counterclockwise direction about the line of sight ('Roll condition') at a constant velocity of 130°/s (Fig. 1b). Still and roll conditions were randomized within a block. Note that the virtual visual target that appeared within the VE remained stationary.

For all experimental conditions, each trial began with the right index finger extended and placed on the sternum (defined as O in Fig. 1a). Subjects were instructed to reach toward the visual target as soon as it appeared in the VE. If the target changed position, the subjects had to move his/her hand towards the new target location (i.e., toward the last target that he/she saw). Subjects were also instructed to keep their hand at the final position till the trial ended, (the scene turned black for 2 s at the end of each trial). No instructions concerning movement speed or accuracy were given.

As seen in Fig. 2, at time $t = 0$, the initial scene appeared. After a random time interval ranging from 1 to 1.5 s, a visual target appeared and at that time the scene remained stationary or started to roll. In the single-step condition, the target remained visible for 2 s. In the double-step condition, following a pre-specified inter-stimulus interval (ISI), the location of the target shifted either left or right (i.e., the central target disappeared and simultaneously a second target appeared) and remained in the new position for 2 s. The target was shifted either before

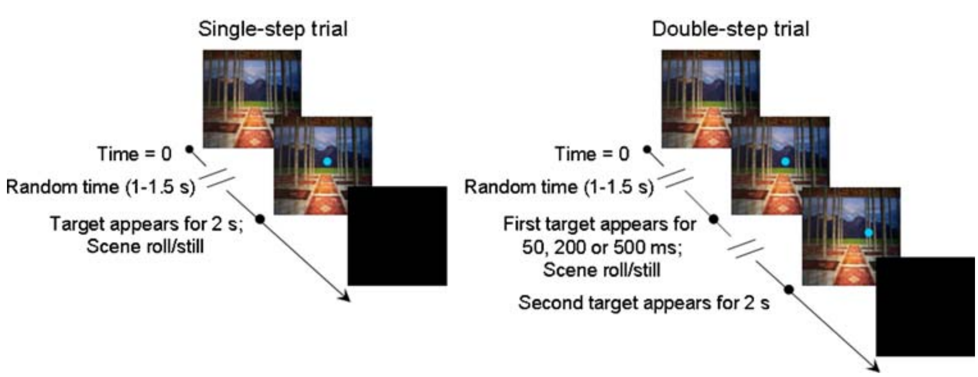

Fig. 2 The double-step paradigm protocol for Experiment 1. Target A and targets A, B are presented for the *left and right panels*, respectively

movement initiation (ISI = 50 or 200 ms) or during the movement (ISI = 500 ms). A total of 40 double-step trials were presented at each ISI. In total, subjects completed 180 trials.

Experiment 2

To explore the possibility that the presence of a visual target throughout the entire trial may lessen the effect of roll motion on performance, Experiment 2 was designed in a similar way to that of Experiment 1, except for the duration of the target appearance. In the single-step condition, a target appeared for only 200 ms. In the double-step condition, the central target appeared and, following a pre-specified ISI (200 or 500 ms), the location of the target was shifted to the left or to the right and remained in the new position for only 200 ms. Thus, subjects were instructed to reach toward the remembered location of the target. The experiment included 5 blocks, each containing a mixture of 12 single-step trials and 16 double-step trials. In total, subjects completed 140 trials.

Data analysis

Data were low-pass filtered off-line at 8 Hz using a fourth order Butterworth digital filter. A 4% tangential peak velocity threshold was used to determine the onset as well as the end of the hand movement. Spatial and temporal kinematic parameters of the reach movement were calculated. These included hand path, reaction time (RT) to initiate a reach, movement time (MT) from movement initiation to movement termination, peak velocity, and the duration of any pauses that occurred during the course of the movement. A pause was defined as an interval of at least 40 ms in which the subject's hand was not moving. Variable and constant errors of the endpoint position of the main hand movement were calculated, and a 95% tolerance ellipse was constructed per trial, using principal component analysis, from the hand position following the main movement termination. The size and shape of the ellipse were characterized by the computed eigenvalues of the covariance matrix (McIntyre et al. 1998). Different trajectory types were identified in double-step movements according to the calculated initial direction of motion, derived at the time of movement onset. For each subject, the distribution of directional hand position was calculated for each singe-step target (A, B and C). The corresponding 95% tolerance ellipses for each single-step target were calculated and used as references for classification of double-step movements.

Statistical analysis was conducted using χ^2 test, two-tailed paired t-test, and two-way repeated measures ANOVA with movement type (single- or double-step) and scene (still or rolling) as within-subject factors. The significance level was set at 0.05.

Results

All subjects accurately reached toward all targets and were able to amend their ongoing arm motion in response to target displacement with both scene conditions. While subjects exhibited single-peaked bell-shaped velocity profiles, without any perturbation of the reach for the single-step movements, the double-step movements were well represented by the double peaked tangential velocity profiles. Furthermore, analysis of the trunk and head position in space revealed no obvious changes during both experiments; therefore, the main focus of the present study is on the arm movement itself where data of the second metacarpophalangeal joint of the right arm are presented. Finally, all subjects reported no feeling of self-motion (i.e., vection).

Reaction time, peak velocity and movement time

The mean value (±SD) of RT to movement initiation was 303 ± 38 ms for Experiment 1 and 320 ± 43 ms for Experiment 2. The mean peak velocity was 2.2 ± 0.6 and 2.2 ± 0.3 m/s for Experiments 1 and 2, respectively. The analysis of both RT and peak velocity showed no significant difference between the single- and double-step conditions. In addition, no significant effect of roll visual motion on RT or on peak velocity was found. However, there was a trend of increasing RT in the presence of roll motion, which approached significance level. By contrast, for both experiments a two-way repeated measures ANOVA (movement type × scene) revealed a significant increase for MT in the presence of roll motion ($F_{(1,10)} = 42.4$, $P < 0.0001$ for Experiment 1; $F_{(1,10)} = 24$, $P = 0.0006$ for Experiment 2). In addition, MT was significantly longer for double-step than for single-step movements ($F_{(1,10)} = 333$, $P < 0.0001$ for Experiment 1; $F_{(1,10)} = 192.4$, $P < 0.0001$ for Experiment 2). On average, double-step movements were larger in amplitude than single-step movements. This might contribute to the observed change in MT between these two conditions (Fig. 3). We further analyzed the effect of roll motion on reaching toward opposite directions by separately comparing single-step movements OB (rightward) and OC (leftward) and double-step movements OAB (rightward) and OAC (leftward), for both experiments. We subtracted MT for still condition from MT for roll condition, and performed a two-tailed paired t-test on the resulting differences resulting from rightward and leftward movements. A significantly larger increase in MT during roll for leftward movements was found; (Experiment 1: single-step,

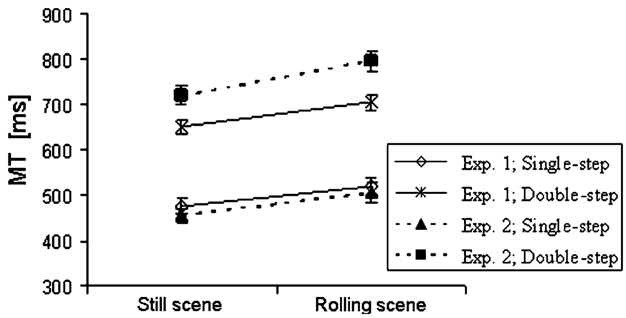

Fig. 3 Mean movement times (with 1 SE) for both scene conditions, presented separately for single-step and double-step movements, in both Experiments 1 and 2

$t_{10} = 2.46$, $P = 0.033$; double-step, $t_{10} = 1.65$, $P = 0.13$; Experiment 2: single-step, $t_{10} = 2.18$, $P = 0.05$; double-step, $t_{10} = 2.5$, $P = 0.031$).

Trajectory analysis

The double-step movement analysis indicated that all subjects exhibited three main types of trajectories, classified according to the initial motion direction (see "Materials and methods"). 'Non-averaged trajectory', the hand moved toward the first target and then changed course during the movement; 'Averaged trajectory', the initial movement direction was intermediate between the first and the second target location; and 'Direct trajectory', the hand moved directly toward the second target location. An example of each trajectory type, made by a representative subject, is shown in Fig. 4a.

The majority of non-averaged trajectories were observed for the longest ISI (i.e., 500 ms) in both experiments. Direct trajectories however occurred mainly during the shortest ISI (i.e., 50 ms) and therefore were observed mostly in Experiment 1. The main effect of ISI on the occurrence of the different trajectory types was evident when all three values of the ISI where taken into account. Therefore, the following analysis on the different hand trajectories is presented here only for Experiment 1. A χ^2 test on the different ISI values (i.e., 50, 200 and 500 ms) showed that subjects had significantly fewer direct and averaged trajectories and more non-averaged trajectories as ISI increased ($\chi^2_{(2)} > 174$, $P < 0.0001$; for both direct, averaged and non-averaged trajectories). These significant changes holds true with both scene conditions. Furthermore, the proportion of the different trajectory types was affected by the presence of roll visual motion, where subject exhibited significantly less direct trajectories during roll condition than during still condition ($\chi^2_{(1)} = 12.2$, $P < 0.001$). For the non-averaged trajectories, an increase which approached significance level was found during roll motion ($\chi^2_{(1)} = 3.7$, $P = 0.06$). The increase in the proportion of the averaged trajectories was not significant, (Fig. 4b). The analysis revealed no obvious difference between rightward and leftward movements.

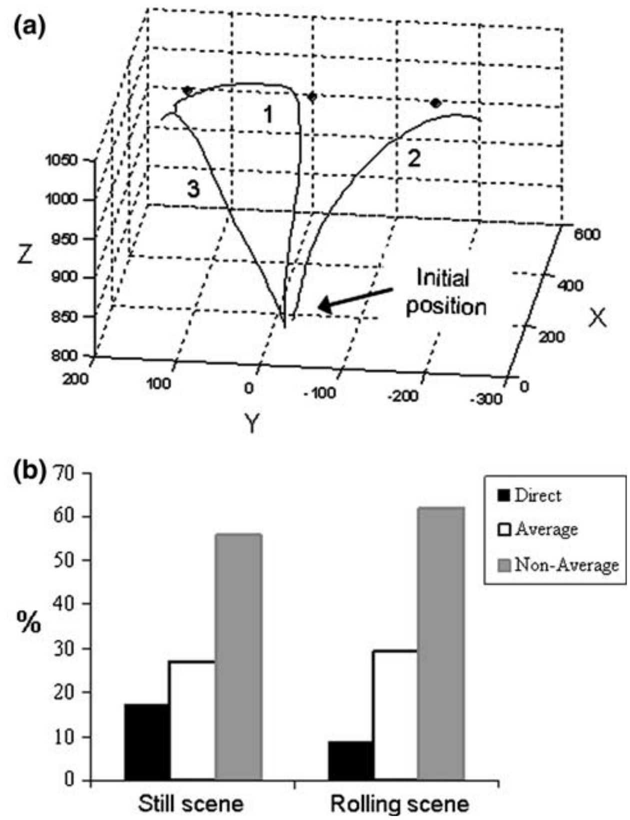

Fig. 4 **a** Representative example of non-averaged, averaged and direct trajectories, labeled as 1, 2 and 3 (for configurations OAC, OAB, and OAC), respectively. Dark circles indicate the target locations. **b** Percentage of direct, averaged and non-averaged trajectories for both scene conditions, for Experiment 1

Paused double-step movements

Further investigation of the temporal parameters of the trajectories revealed that for all subjects, some of the double-step movements contained a pause prior to modifying trajectory direction. An example of a path and the corresponding tangential velocity profile of a paused modified movement are shown in Fig. 5a. For all subjects, pause modified movements were observed only for the longest ISI (i.e., 500 ms). The proportion of paused movements calculated from the total of double-step movements was lower for Experiment 1 (13.7%) compared to Experiment 2 (24%). In addition, mean paused movement duration of 124 ms and 136 ms was found for Experiments 1 and 2, respectively. Strikingly, paused movements were also affected by the presence of roll visual motion. Although the proportion of paused movements was similar in both scene conditions for both

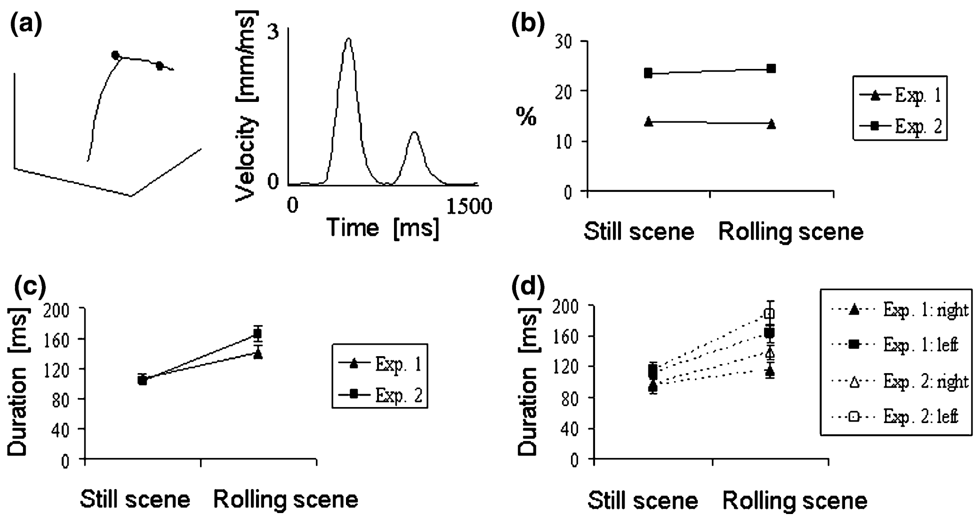

Fig. 5 **a** Example of a 3D path and the corresponding tangential velocity profile of a paused movement (for configuration OAB). Subject paused for 180 ms. *Dark circles* represent the target locations. **b** Percentage of paused movements and **c** paused movement duration (mean ± 1 SE) for both scene conditions, for Experiments 1 and 2. **d** Paused movement duration (mean ± 1 SE) separated for rightward and leftward double-step movements (configurations OAB, OAC, respectively)

experiments (Fig. 5b), the duration of the pause was significantly increased for the rolling scene compare to the still scene in both experiments (142 vs. 107 ms for Experiment 1, $\chi^2_{(1)} = 4.9$, $P = 0.027$; 166 vs. 104 ms for Experiment 2, $\chi^2_{(1)} = 14.2$, $P < 0.0001$). The difference in pause duration between the two experiments was mostly evident in the roll condition (Fig. 5c). As for the MT, we further analyzed the effect of roll motion on paused movement duration for reaching toward opposite directions. Whereas no significant difference was found for the still condition, paused movement duration significantly increased for leftward compare to rightward movements during roll (Fig. 5d). This holds true for both experiments; (115 vs. 164 ms for Experiment 1, $\chi^2_{(1)} = 8.6$, $P < 0.003$; 139 vs. 189 ms for Experiment 2, $\chi^2_{(1)} = 7.62$, $P < 0.006$).

Endpoint variability

Analysis of both constant and variable errors of the endpoint position of the main movement was performed for each target position in both scene conditions. All subjects exhibited measurable constant errors, where both overshoots and undershoots with respect to the subject's body were observed. As one may expect, endpoint variability was higher for Experiment 2 compared to Experiment 1 (for variable errors: $F_{(1,42)} = 19.8$, $P < 0.0001$; for constant errors: $F_{(1,42)} = 3.4$, $P = 0.07$). However, the observed increase of both constant and variable errors during roll was not significant, for both experiments (Fig. 6). No significant difference was found between single- and double-step conditions and between rightward and leftward movements.

Terminal arm posture

As mentioned earlier, we instructed our subjects to keep their arm at the final position until the trial ended. While subjects did not exhibit any significant trunk movements throughout the trial, changes in the terminal arm posture were observed. To quantify any changes in hand position that might occur, a 95% tolerance ellipse was constructed per trial, from the hand position following the main movement termination, (i.e., from the time of movement offset till the end of the trial). Results indicated that all subjects kept their hand at the final position for both scene conditions in Experiment 1, for both single- and double-step movements. By contrast, all subjects exhibited an obvious change in hand position during roll in Experiment 2. This was seen for

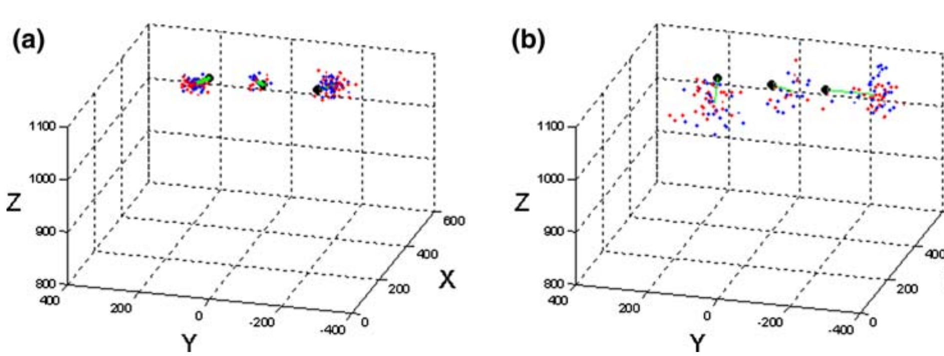

Fig. 6 Constant errors and variability of the endpoint position of the main hand movement. Examples from a single subject who performed during still (*red dots*) and roll (*blue dots*) conditions in **a** Experiment 1 and **b** Experiment 2. Targets appear as *black circles*. *Green lines* represent the constant errors

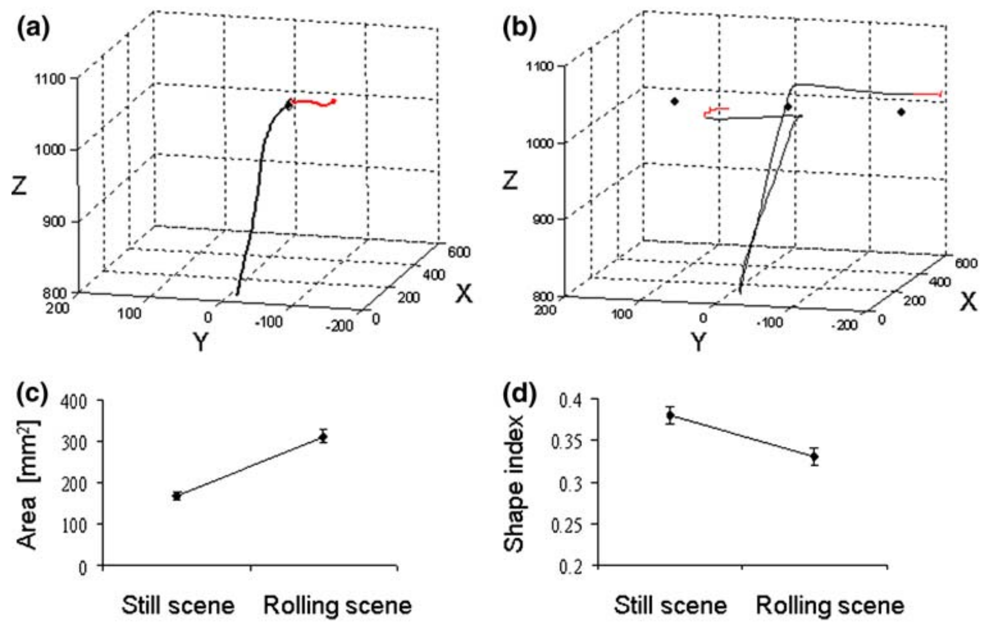

Fig. 7 Typical 3D paths during roll condition in Experiment 2 showing the main hand movement (in *black*) followed by additional hand movement (in *red*), for **a** single-step (configuration OA) and **b** double-step (configurations OAB, OAC) movements. Targets appear as black circles. **c** Mean area (± 1 SE) and **d** shape (mean ± 1 SE) of the 95% tolerance ellipse, for both scene conditions, for Experiment 2

both single- and double-step movements where, following termination of the reaching movement, the hand continuously moved slowly toward the right which was opposite the direction of the rolling scene. Examples of 3D paths showing the main movement followed by additional movement of the hand are depicted in Fig. 7a, b. Furthermore, following both rightward and leftward movements, the hand slowly moved toward the right (Fig. 7b).

The analysis of the size and shape of the tolerance ellipse, presented here only for Experiment 2, showed a clear effect of the roll visual motion. A two-tailed paired t-test showed both significant increase in the mean ellipse area ($t_{10} = 7.08$, $P < 0.0001$) and significant decrease in the mean shape of the ellipse ($t_{10} = 2.7$, $P = 0.02$) for roll condition compared to still condition (Fig. 7c, d). Furthermore, the mean constant error for the drift component significantly increased during roll ($t_{10} = 6.7$, $P < 0.0001$).

Experiment 3

The first two experiments demonstrated that both temporal and spatial aspects of the reach movement were affected by the presence of roll motion. The purpose of this experiment was to examine the effect of manipulating the direction of visual motion on reaching and terminal arm posture, where we predicted a mirror image pattern of our results for rotation in the opposite direction.

Materials and methods

Nine new subjects (four males, five females; aged 20–38 years) completed Experiment 3. Six of them (3 males, 3 females) completed two additional blocks (half of Experiment 3), where in these blocks they reached toward targets with their left arm. Subjects gave informed consent in accordance with the Institutional Review Board of Temple University.

The same VE as in Experiments 1 and 2 was used in this experiment. The VE was projected via two Panasonic PT-D5600U DLP-based projectors onto a 2.0 m × 2.8 m back-projection screen. Each projector throws a full-color stereo workstation field (1,024 × 768 stereo) at 60 Hz onto the screen. Different polarized filters placed in front of the projectors provided a left eye and right eye view of the image, and “passive” stereo glasses worn by the subject delivered the correct view to each eye. (The glasses limited the subject’s horizontal and vertical fields of view to 100° and 55°, respectively). Same Motion Analysis system was used with reflective markers attached to the subject’s head (for updating the correct perspective and stereo projections for the scene), and one reflective marker attached on the second metacarpophalangeal joint of the arm. Procedures were the same as in Experiment 2, however, for the roll condition the scene could now roll clockwise (CW) or counterclockwise (CCW). Experiment 3 was divided into four blocks where in total, subjects completed 216 trials.

Results

Since part of the apparatus used in this experiment was new (e.g., the projectors), we first confirmed that CCW roll motion affected reaching and terminal arm posture in the same way as was found for Experiment 2. Thereafter, we compared trials from the three different scene conditions (i.e., still, CW roll and CCW roll). The analysis revealed that both CW and CCW roll motions affected reaching. A two-way repeated measures ANOVA (movement type × scene) revealed a significant increase for MT in the presence of roll motion ($F_{(2,16)} = 13.5$, $P = 0.0004$) for single- and double-step conditions, where both CW and CCW roll conditions were significantly different than the still condition. Furthermore, a significant increase in pause movement duration in the presence of roll motion was found ($F_{(2,220)} = 11.2$, $P < 0.0001$), where both CW and CCW roll conditions were significantly different than the still condition. In addition, the analysis on reaching toward opposite directions revealed the predicted mirror image pattern of our results for the CW rotation. For double-step movements, a significantly larger increase in MT during CCW roll for leftward movements was found ($t_8 = 4.3$, $p = 0.003$), and a larger increase in MT during CW roll for rightward movements approached significance level ($t_8 = 2.2$, $P = 0.06$). The observed increase in MT for single-step movements however was not significant. Moreover, whereas no significant difference was found for the still condition, paused movement duration significantly increased for leftward compared to rightward movements during CCW roll (138 vs. 86 ms, $\chi^2_{(1)} = 12.1$, $P < 0.001$), and significantly increased for rightward compared to leftward movements during CW roll (139 vs. 107 ms, $\chi^2_{(1)} = 4.2$, $P = 0.04$). By contrast, the analysis of the terminal arm posture did not reveal a mirror image pattern of our results. While all subjects exhibited a hand drift following the main reaching motion in the presence of roll motion (revealing a significant change in the area and shape of the tolerance ellipses compared to the still condition), the hand drifted toward the right during both CW and CCW roll motions. To further examine this unpredicted phenomenon, six of the nine subjects completed two additional blocks while reaching with their left arm. The results in this case revealed that subjects tended to let their left hand slowly drift toward the left, irrespective of the direction of visual motion.

General discussion

The aim of the current study was to evaluate online visuomotor control of movements within a dynamic virtual environment in order to investigate the effect of roll motion of the visual scene on planning and execution of simple and complex reaching movements, using the double-step reaching task. We assumed that roll motion of the scene would affect reaching as it was previously found to produce robust perceptual effects and postural changes. The main findings that emerged from the present study indicated that both temporal and spatial aspects of the reach movement were affected by the presence of roll motion. The most striking effect on the control of goal-directed movements was interference in the ability to update the motor plan in response to target displacement.

Efficiency of visuomotor control in the VE

Earlier studies which investigated reach-to-grasp movements in VE have demonstrated that subjects used similar movement strategies during physical and virtual reaching and grasping (Kuhlen et al. 2000; Viau et al. 2004). For example, Viau et al. (2004) showed that arm movement trajectories of both healthy subjects and individuals with mild hemiparesis following stroke were smooth and followed similar paths during reaching, grasping and placing a ball in both virtual and real physical environments. In accordance with these earlier studies, we have previously reported that subjects were able to reach toward all single- and double-step targets as well as to amend their ongoing movement in response to the unpredictable target displacement, while performing in the VE (Dvorkin et al. 2007). Whereas similar behavior during a double-step task has been shown in the past for reaching within a stable VE (Martin et al. 2003), we have now demonstrated that this holds true for both the still and dynamic scene conditions. Arm movements toward visual targets are controlled by processing information relative to hand and target positions (Desmurget et al. 1998). However, changes in the spatial relationship between the hand and the goal position of the reach may occur at any time. Our data suggest that reaching toward a virtual target within the rotating VE was programmed and controlled in a similar way to that of a physical world, showing comparable timing and kinematic modifications. It is important to mention that this holds true for both Experiments 1 and 2, that is, for reaching toward a visible virtual target (Experiment 1) as well as toward a briefly presented target (Experiment 2). Martin et al. (2003) proposed that a moving visual background might have a deleterious effect on visuomotor coordination due to changes in the subject's reference frames. Our results however, emphasize that the presence of roll motion of the VE did not have such a harmful effect on both simple and complex reaching movements. Yet subjects in the present study were seated and were exposed to only one constant velocity of the scene, which rolled for a short time. Thus, it would be of interest to further manipulate the velocity of the background motion in a future study.

Effects of roll visual motion on reaching

Compared to a stationary environment, reaching within a dynamic environment involves additional sensorimotor transformations as a result of the continuous change in the visual reference frame, (i.e., increasing the computational complexity). This requires the visuomotor system to continuously update spatial representations in order to accurately act on the world around us, which may result in additional delay in the control processes, and hence adversely affect some aspects of performance. The continuous updating could affect any of the following processes; the target localization, movement planning and movement execution. The double-step task is interesting in this regard as it involves updating of both visual and motor processes. Our findings reflect the effect of an increase in computational complexity on performance, showing a clear effect of roll motion on both the spatial and temporal aspects of movement, as well as on planning and execution of the reaching movement, especially the double-step movements. This was evident from changes in proportion of the different trajectory types and significantly longer MT and paused movement duration in the presence of roll motion. Furthermore, movements that were directed with the roll direction (e.g., leftward movements during CCW roll motion) were affected more than those directed against the roll direction.

Different trajectory types have been demonstrated in the past using the double-step task for both young and elderly healthy subjects, for saccadic eye movements (Aslin and Shea 1987; Becker and Jurgens 1979) and for reaching in both 2D and 3D space (e.g., Bonnefoi-Kyriacou et al. 1998; Dvorkin 2004; Gréa et al. 2002; Henis and Flash 1995; Van Sonderen et al. 1989). However, in these studies, movements have only been tested in stationary visual environments so that the subjects did not need to modify their motor plan in response to changes in the visual space. In the current study we showed that all subjects exhibited all three types of trajectories (i.e., direct, averaged and non-averaged) for both scene conditions. More importantly, however, we observed a significant change in the proportion of direct and non-averaged trajectories in the presence of roll visual motion. Earlier investigations on the double-step reaching task have suggested that the initial trajectory plan toward the first target continues unmodified until its intended completion, and an additional trajectory plan toward the second target is superimposed on the first one to yield the plan for the entire modified trajectory (Flash and Henis 1991; Henis and Flash 1995). Changes in proportion of the type of movement being generated during roll motion may reflect the use of a compensatory strategy to accommodate changes in the spatial relationship between the hand and the moving visual scene. Note however, that RT (i.e., movement initiation) was not affected by roll visual motion. We suggest that roll motion affected the temporal and spatial parameters used to appropriately scale the underlying superimposed elemental movements, thus, interfering with the ability to plan in parallel the two motor vectors of the movement.

Further evidence for the interference in updating the motor plan comes from the temporal kinematics of double-step movements, as was seen from the changes in paused movement duration. Previous reaching studies which used stationary visual environments have reported paused movements for both healthy subjects and stroke and Parkinson's disease patients (Dvorkin 2004; Krebs et al. 1999; Plotnik et al. 1998). It was shown that for healthy adult subjects on average, paused movements occurred in 15% of the double-step movements, with a mean duration of 200 ms. Our findings are consistent with these previous results, however, the observed increase in pause duration during the double-step reach when combined with roll motion was striking, suggesting that the complexity of the task enhanced the interference with the ability to integrate the responses to the two successive visual targets.

Analysis of the effect of roll motion on reaching toward opposite directions revealed further intriguing discrepancies. Increased changes in both MT and pause movement duration for movements that were executed in the direction of roll motion (i.e., leftward movements during CCW roll and rightward movements during CW roll), suggests that background roll of the visual scene affected reaching differently when subjects reached with or against roll direction. Our findings are in accordance with the findings of an earlier study which investigated the effect of background motion during a smooth pursuit eye movement on reaching (Whitney and Goodale 2005). In their study, the authors indicated that subjects reached more accurately when retinal image motion was opposite to the direction of pursuit than when the background moved with the pursuit. We did not record the eye movements in our study, but it is possible that the changes we observed were related to an effect of visual scene motion on eye-hand coordination.

Apart from these findings, it should be mentioned that unlike recent studies which investigated arm movement control during whole-body rotation (e.g., Bresciani et al. 2002; Lackner and DiZio 1998), we did not observe disrupted movement trajectory and endpoint. Although we observed an increase in endpoint variability during roll, this was not significant, which suggests that subjects were able to amend their ongoing movements efficiently even in the presence of roll motion. It has been argued by Lackner and DiZio that the inertial Coriolis forces generated by reaching movements in a rotating environment initially induced these errors (for review, see Lackner and DiZio 2005). The difference in our observations may have been due to the fact that our subjects were seated on a stable stool during the exposure to roll visual motion of the scene, whereas in these recent studies, subjects themselves were passively rotated during movement planning and execution, that is, they had to further modify their motor plan with regard to the generated forces. Cohn et al. (2000) on the other hand reported deviated paths and endpoints for reaching during exposure to yaw visual motion which induced illusion of self-rotation. In their experiment, however, subjects were exposed to rotation of 2 min and never received any feedback about hand position or whether they hit the target.

Another issue that warrants consideration is the observed difference in performance between Experiments 1 and 2, where the most profound change was evident from the occurrence of paused movements (see Fig. 5). We had hypothesized that the appearance of a visual target within the VE throughout the entire trial might reduce the effect of roll motion on reaching performance. Thus, on each trial in Experiment 2, the final target was visible for a period of 200 ms. Indeed, the stronger effect of roll motion in Experiment 2, indicates that the presence of a stable focal image (i.e., the target) within the VE helped the subjects to suppress the effect from background motion of the visual field. This held true for both CW and CCW roll motions (Experiment 3).

A final issue we would like to address is the effect of roll visual motion on RT. It is interesting to note that while no significant effect was found for RT, anecdotal reports suggest that subjects felt as if their reaction time was prolonged during roll motion compared to the still scene. Performing accurately in a dynamic environment requires adaptation and adjustment to its spatial and temporal characteristics (Schubotz et al. 2000). One possibility is that the roll visual motion affected the subjects' perception of the time required for preparation of the motor output. This hypothesis can not currently be verified, but designing an experiment in which the velocity and timing of the roll visual motion is being manipulated might shed light on this assumption.

Effects of roll visual motion on posture

Further evidence for the effect of roll motion combined with the absence of a stable focal image on behavior comes from the analysis of the arm position in space. While subjects did not exhibit significant changes in head and/or trunk movements during roll motion of the scene compared to the still condition, changes in the terminal arm posture were observed when the final target was visible for only 200 ms. The analysis of Experiment 2 revealed that following the main reaching motion subjects tended to let the hand slowly drift toward the right, in the direction opposite of the rolling scene. This corresponded with the significant change in the area and shape of the tolerance ellipses during the roll condition. By contrast, the analysis of the variable and constant errors of the endpoint position of the main movement indicated no such change. This suggests that the hand drift was not present in the main structure of the movement but occurred once the hand deceleration has reached a given threshold. Manipulating the roll motion direction (Experiment 3) revealed further intriguing findings. Whereas the right arm drifted to the right during both CCW and CW roll motions, the left arm slowly drifted toward the left, irrespective of roll direction. The observed hand drift cannot be explained by muscle fatigue since it did not occur during the still condition. Furthermore, although holding the arm in space (against gravity), the drift was directed rightward or leftward but not downward. Arm position drift during a reaching task has been reported in the past, where such drift has been attributed to changes in the use of proprioception as a source of limb position information in the absence of visual feedback (Brown et al. 2003; Moisello et al. 2008). Furthermore, it has been suggested that when estimating the arm position in space, the central nervous system weights the visual and proprioceptive feedback differently depending on the computation being performed (Sober and Sabes 2003, 2005). In the current study the moving arm was visible throughout the entire trial. However, the hand drift occurred while the VE was rotating and there was no static frame of reference within the VE to rely on, (the target disappeared after 200 ms in Experiments 2 and 3). It is possible that the presence of the moving visual field produced a reduced reliance on visual feedback and an increased dependence on proprioceptive information to estimate arm position in space. These changes in the use of proprioception combined with the absence of a stable frame of reference could contribute to inability to maintain a stable arm position in space. Additionally, the emergent drift direction depended upon which arm was used suggesting that drift was generated by the mechanical properties of the arm. One possibility is that following the main movement termination the arm moved toward a more preferred position in space which does not involve crossing the body midline.

Overall body posture was not affected in our experiments. Previous studies have demonstrated strong effects of background motion of the visual field on the postural response of subjects (e.g., Dijkstra et al. 1994; Keshner et al. 2006; Previc 1992). It is assumed that posture is altered due to conflicting sensory information. For instance, during an upright stance, a sensory conflict may arise from the roll motion of the visual field while the body itself is stationary. In the present study, subjects were exposed to roll motion that lasted for about 2 s while sitting on a stable stool with their feet in full contact with the floor. Thus, it is likely that the more stable posture together with input cues from the support surface helped the subjects maintain a steady body orientation in space.

In the case of non-constraint reaching movements, posture and arm movements must be coordinated in order to achieve the motor goal, keeping an accurate movement while maintaining an appropriate posture (Massion et al. 2004). During reaching from an upright position, complex whole-body movements might take place. Hence, we predict that reaching during exposure to roll motion while standing would yield a somewhat different postural behavior pattern than the one observed in the current study, showing less hand drift and more motion of different body segments such as the head and/or trunk (unpublished data, 2008).

Conclusion

There is ample evidence that the central nervous system reacts to perturbations by online adjustments of both movement and posture. However, performance on a more demanding task such as the double-step task combined with the exposure to wide field-of-view visual motion could highlight the underlying control mechanisms involved in achieving the goal of the movement. In this study, we demonstrated that roll motion of the visual field affected both planning and execution of the reaching movement, but particularly interfered with the updating of goal-directed movements in response to target displacement. These effects on the control processes however were not deleterious, suggesting that the central nervous system controls for continuous changes in the spatial relationship between the hand and the goal position of the reach in an efficient way. Future studies need to further verify this issue by manipulating both the velocity and timing of the background visual motion. The present study established baseline capabilities of human performance within a dynamic environment and has implications for different populations such as elderly subjects who have demonstrated impairments in online control of reaching movements compared to young adults (Sarlegna 2006), and neurologically impaired individuals who demonstrate increased instability in dynamic environments (e.g., Keshner and Kenyon 2004).

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