Experimental Brain Research (2019) 237:793–803
https://doi.org/10.1007/s00221-018-05462-2

RESEARCH ARTICLE

Adaptation and spatial generalization to a triaxial visuomotor perturbation in a virtual reality environment

Catherine Lefrançois[1] · **Julie Messier**[1,2]

Received: 2 February 2018 / Accepted: 21 December 2018 / Published online: 3 January 2019

Abstract

We explored visuomotor adaptation and spatial generalization of three-dimensional reaching movements performed in a virtual reality environment. We used a multiphase learning paradigm. First, subjects performed reaching movements to six targets without visual feedback (VF) (pre-exposure phase). Next, participants aimed at one target with veridical VF (baseline phase). Immediately after, they were required to adapt their movements to a triaxial visuomotor perturbation (horizontal, vertical, and sagittal translations) between actual hand motion and VF of hand motion in the virtual environment (learning phase). Finally, subjects aimed at the same targets as in the baseline (aftereffect) and pre-exposure phases (generalization) without VF (post-exposure phase). The results revealed spatial axis-dependent visuomotor adaptation capacities. First, subjects showed smaller intertrial variability along the horizontal compared to the sagittal and vertical axes during the baseline and learning phases. Second, although subjects were unaware of the visual distortion, they adapted their movements to each component of the triaxial perturbation. However, they showed reduced learning rate and less persistent adaptation (aftereffect) along the vertical than the horizontal and sagittal axes. Similarly, subjects transferred the newly learned visuomotor association to untrained regions of the workspace, but their average level of generalization was smaller along the vertical than the horizontal and sagittal axes. Collectively, our results suggest that adapting three-dimensional movements to a visual distortion involves distinct processes according to the specific sensorimotor integration demands of moving along each spatial axis. This finding supports the idea that the brain employs a modular decomposition strategy to simplify complex multidimensional visuomotor tasks.

Keywords Movement adaptation · Spatial generalization · Visuomotor perturbation · Reaching movement · Kinematic · Virtual reality

Introduction

The plasticity in sensorimotor circuits of the brain allows us to flexibly adapt movements to various contexts. Adapting a mastered motor skill to new demands, such as reaching with a hammer or a computer mouse, requires the acquisition of novel visuomotor associations. Our ability to learn novel arbitrary visuo-proprioceptive associations is a crucial aspect of efficient everyday motor actions, especially if it generalizes to unfamiliar contexts or spatial regions without further training. Spatial generalization refers to the extent to which a newly learned visuomotor association within a specific region of space transfers to different untrained spatial regions.

Visuomotor adaptation and generalization skills have been intensively studied using a variety of reaching paradigms where participants aimed at a visual target with distorted visual feedback of their hand position. Converging evidence demonstrated that these adaptive processes are tightly linked to the context in which movements are performed (Desmurget et al. 1997; Michel et al. 2007; Krakauer et al. 2000; Taylor and Ivry 2013). Several factors related to the reaching task features and training conditions such as the type (e.g., translation or rotation), the size and awareness of the visuomotor distortion as well as the spatial arrangements

---

✉ Julie Messier
j.messier@umontreal.ca

[1] École de kinésiologie et des sciences de l'activité physique, Faculté de médecine, Université de Montréal, 2100, boul. Édouard-Montpetit, bureau 8225, Montreal, QC H3T 1J4, Canada

[2] Institut universitaire de gériatrie de Montréal, Université de Montréal, Montréal, QC, Canada

of the training and generalization targets have been shown to impact on adaptation and generalization capabilities (Kagerer et al. 1997; Shabbott and Sainburg 2010; Taylor and Ivry 2013). In the present study, we explored visuomotor adaptation and spatial generalization in the context of natural unconstrained three-dimensional reaching movements. This is noteworthy as the vast majority of everyday life's movements are performed in a 3D workspace.

One critical factor of three-dimensional reaches that might affect our ability to learn and transfer a novel visuomotor association is the biomechanics of the movements. Almost all previous studies assessing visuomotor adaptation and spatial generalization have used 2D tasks involving movements restricted to the horizontal plane. However, three-dimensional movements are biomechanically more complex than planar movements. They involve more degrees of freedom to be controlled as well as compensation for the gravitational force field which increases the proprioceptive processing demand. Of particular relevance, it was suggested that the contribution of vision and proprioception to arm movement planning in the vertical plane is linked to the multisensory and biomechanical demands associated with moving against gravity (Apker et al. 2011). Furthermore, one recent study by Toma et al. (2015) suggested that gravity strongly influences visuomotor adaptation to a visual rotation. However, since these previous reports involved movements performed along a single plane they do not provide direct insights on how natural 3D movements are adapted along the vertical axis.

Another important feature of natural unconstrained 3D reaches is that they often require simultaneous adaptation along all three axes of 3D space (e.g., using a novel tool). However, most anterior studies of visuomotor adaptation to a translational shift of the visual feedback have used a perturbation applied along a single axis of the workspace (Ghahramani et al. 1996; Heuer and Sülzenbrück 2012; Vetter et al. 1999). In one study, subjects were exposed to either a horizontal or a sagittal visuomotor translation in separated experiments involving planar movements (Ghahramani et al. 1996). They showed faster rate of adaptation to the horizontal than the sagittal translational shift suggesting that adaptation along these two axes may take place through distinct independent neural processes.

Moreover, in two previous reports of 3D movements, we used a translational shift applied simultaneously either to two axes (biaxial perturbation, horizontal, and vertical) or three axes of 3D space (triaxial perturbation) to test visuomotor adaptive skills of healthy subjects and patients suffering from Parkinson's disease (Messier et al. 2007; Mongeon et al. 2013). All subject groups tended to show a slower rate of adaptation when compensating for the vertical component of the perturbation. This suggests that adapting 3D movements along the vertical axis might represent a more challenging condition than movement adaptation along the horizontal and sagittal axes. However, the rate of adaptation to the horizontal, sagittal, and vertical component of the visuomotor perturbation was not directly compared and also importantly, spatial generalization of visuomotor adaptation was not assessed in these prior studies.

In the current study, we used a 3D virtual reality environment to introduce a gradual triaxial visuomotor perturbation, i.e., a progressively increasing translational shift of the visual feedback applied simultaneously along the horizontal, sagittal, and vertical axes. The goal of this study was to compare the rate and magnitude of adaptation to the horizontal, sagittal, and vertical component of a triaxial perturbation and to assess whether such visuomotor adaptation generalizes to different spatial regions of the three-dimensional workspace.

Based on previous work, we expect different adaptation learning rate to the three components of the triaxial perturbation. Specifically, we predict faster adaptation to the horizontal compared to the sagittal and vertical components of the triaxial visual distortion, with the slowest adaptation rate along the vertical axis. In a similar vein, we predict that subjects will generalize adaptation along all three spatial axes, but that the magnitude of the spatial generalization will be the greatest along the horizontal axis, intermediate along the sagittal axis, and the lowest along the vertical axis.

The assessment of visuomotor adaptation and spatial generalization skills using natural 3D movements as well as a perturbation that simulate everyday visuomotor challenges might provide a more complete portrait of human adaptation and generalization capabilities. Furthermore, investigating the plasticity of the visuomotor system using more real-world situations is of basic importance to understanding the central nervous system and to develop knowledge for sport training and rehabilitation of movement disorders.

Methods

Subjects

Fourteen university students (mean age 23.1, SD 2.7 years) participated voluntarily in this study. All participants had normal or corrected-to-normal vision and were right-handed, measured by the Edinburgh Handedness Inventory (Oldfield 1971). The experimental protocol was approved by the institutional review board of the University of Montreal. Participants were not informed about the specific purposes of the study and no information was provided about the visuomotor perturbation applied in the virtual reality (VR) world.

Experimental procedure

Subjects sat in the dark in front of the virtual reality system (Fig. 1). A specialized software (IST, inc.) was used to present the VR visual scene, to calibrate the VR world and to monitor arm movements using an Optotrak Certus motion capture system (NDI, Inc.). Subjects wore stereoscopic glasses (Crystal Eyez, Stereographic inc.) to view the virtual three-dimensional scene. The VR world was calibrated before each session so that the participant had a coherent stereo visual input and to ensure that the VR scene was continually adjusted to the subject's head movements (refreshing rate 120 Hz). This calibration was achieved by both the initial measurements of the subject's inter-pupillary distance and viewpoint (point directly between the two eyes) and the continuous monitoring of signals from four infrared-emitting diodes (IREDs) fixed on the stereoscopic glasses. Finally, the position of the hand was recorded by signals from an IRED positioned on the right index fingertip.

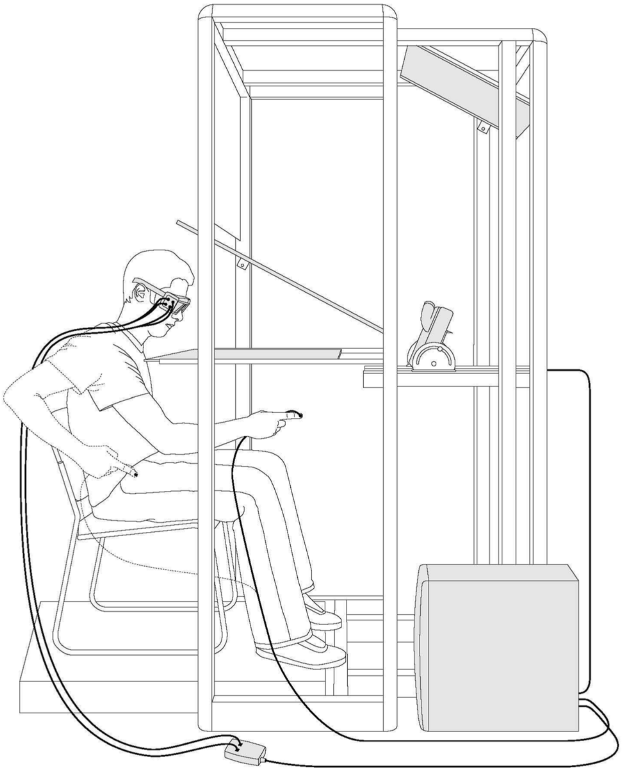

Fig. 1 Schematic representation of the experimental setup. The subjects sat on a chair facing the 3D virtual display. Looking down at the semi-transparent mirror through stereoscopic glasses, the subject sees the virtual image of the targets as well as the 3D reconstruction of their hand trajectory

The learning target was positioned at 8 cm rightward (‘*x*’ axis) relative to the center of the mirror of the virtual display, 43 cm along the sagittal plane (‘*y*’ axis) and 15 cm below the mirror (‘*z*’ axis). This particular target location was chosen for several reasons. First, hand displacement was sufficiently large and unfolds in the three spatial planes. The average hand displacement for a typical subject was 11 cm, 33.5 cm, and 20.5 cm from the start position along the horizontal (*x*), sagittal (*y*), and vertical (*z*) axes, respectively (3D distance = 40 cm). Second, subjects never had to fully extend their arm while aiming during the learning session and the pre- and post-exposure phases. Finally, the subjects' hand never crossed the midline during the learning session which would have increase the likelihood that the visual distortion be consciously detected.

The experimental session consisted of a series of phases (Table 1). The first was a “familiarization” phase in which participants performed reaching movements to four targets in the VR world until they demonstrated a clear understanding of the task (5–10 trials per target). The familiarization targets were distributed in the same spatial workspace but at different spatial positions than those used in the experimental session. A piece of sandpaper (1.5 cm^2) placed on the subject's right thigh at a distance of 10 cm from the hip served as the start position of each movement. Since the experiment took place in the dark and the start position was not in the natural visual field, subjects never had direct vision of their hand or fingertip position during the experimental session.

Each trial began with the presentation of a green target (1 cm sphere) for 1 s in the VR scene. Immediately after, an auditory signal instructed subjects to reach out to the remembered target location to hold their final hand position at the estimated target location for 1 s before returning their hand to the initial position. After each movement, a 3D

Table 1 Experimental protocol

Experimental phases	Number of targets	Number of trials	Block number
1. Familiarization phase	4 targets	20–40 trials	–
2. Pre-exposure phase	6 targets	30 trials	–
3. Baseline phase	1 target	12 trials	Block 1
4. Leaning phase	1 target	90 trials	Block 2–10
5. Post-exposure phase			
(a) Aftereffect	1 target	5 trials	Block 11
(b) Generalization	6 targets	30 trials	–

reconstruction of the subject's hand trajectory and final hand position was shown simultaneously with the target location for 2 s. The target appeared as a virtual three-dimensional green sphere and the trajectory of the hand was presented in a static form as a series of white dots (10/s) that match the actual handpath in space with a red sphere (1 cm) indicating the reaching endpoint.

After this hand trajectory feedback, subjects were required to return to the initial start location. Subjects were instructed to use the visual feedback of the previous trial to enhance their accuracy on the next trial, i.e., to point to the spatial position that would minimize the distance between the red and green spheres along the horizontal, sagittal and vertical axes. There was no instruction to initiate movements rapidly, which might have influenced reaction time. Subjects were encouraged to perform a single direct uncorrected reach at a natural speed with their right index extended to place their index fingertip at the memorized target location as accurately as possible.

The second phase consisted of "pre-exposure" trials during which subjects completed thirty reaches aimed at six targets presented in a pseudo-random order (five trials per target). The pre-exposure targets were distributed around the learning target, i.e., they were positioned on each side of the learning target at a distance of 8 cm along the horizontal, sagittal, and vertical spatial axes (Fig. 2a). However, in contrast to the familiarization phase, no visual feedback was provided to the subjects after their movements. This allowed us to measure their initial accuracy level while aiming to these specific spatial locations, before any learning took place in the VR environment.

The third and fourth phases were "baseline" and "learning" trials (Fig. 2b). In the baseline (block 1), subjects performed 12 reaches aimed at the learning target in absence of any perturbation and received veridical visual feedback about their hand trajectory after the movement. The learning phase consisted of 90 reaches divided into nine blocks of ten trials (block 2–10). Subjects first performed 60 trials (6 blocks) while exposed to a gradually increasing triaxial visuomotor perturbation. Accurate compensation for the visual distortion thus required movement adaptation along the horizontal, sagittal, and vertical axes. This involved learning a new association between the hand trajectory feedback presented in the VR scene after the movement and the actual hand displacement sensed using proprioception. The perturbation was introduced gradually in small steps over the course of the first six learning blocks (blocks 2–7) such that subjects never experienced large movement errors (increasing in small undetectable steps). At the beginning of these learning blocks, the perturbation shifted the hand trajectory feedback 1.3 cm to the left, 1.3 cm further and 1.3 cm higher than the hand trajectory feedback provided in the previous block of trials such that the veridical hand trajectory was displaced by 7.8 cm along each spatial axis at the end of the first six learning blocks (3D displacement of hand trajectory = 13.5 cm). The learning phase terminated with three additional blocks of 10 trials (block 8–10) during which subjects were exposed to the perturbation at full scale. This stepwise gradually increasing visuomotor perturbation paradigm was chosen to investigate learning and generalization because it generally produces more complete adaptation as well as larger aftereffects than a sudden perturbation onset (Kagerer et al. 1997; Michel et al. 2007; Saijo and Gomi 2010). Furthermore, greater transfer of learning from one context to another was observed after gradual learning (Kluzik et al. 2008).

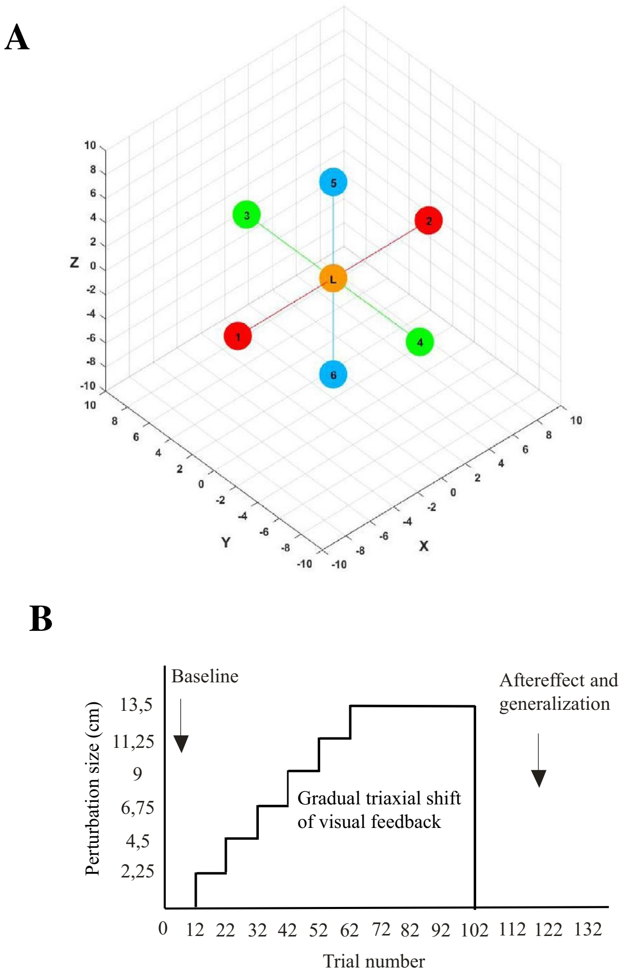

Fig. 2 Representation of target locations in the 3D space (**a**) and the experimental protocol (**b**). The centered target "L" represents the learning target used during all experimental phases, while the targets 1 through 6 were used for the generalization test

Finally, the learning phase was followed by a post-exposure phase including both the aftereffect and generalization trials. In the aftereffect and generalization trials, participants performed reaching movements in absence of any visual perturbation and no visual feedback of their hand trajectory was provided as in the pre-exposure phase. In the aftereffect trials (block 11), participants completed five reaches aimed at the training target, whereas in the generalization trials, they performed five reaches to each of the six pre-exposure targets. The learning as well as the six pre-exposure targets were presented in a pseudo-random order. Although, aftereffect and generalization trials were combined during the post-exposure phase, they were analyzed separately to assess learning (aftereffect trials, training target) and spatial generalization (pre-exposure targets).

Kinematic recording and data analysis

The 3D spatial coordinates of the IRED placed on the right index fingertip were sampled at a rate of 160 Hz with a motion analysis system (2 Optotrak Certus, Northern Digital, Inc., Waterloo, Ontario, Canada). The times series of IRED coordinated were then digitally low-pass filtered with a Butterworth filter with a cut-off frequency of 8 Hz. Customized analysis software (Matlab, The Mathworks, inc.) was used to display and process trials. Movement onset was defined as the first time the 3D index fingertip velocity exceeded 3% of index fingertip peak velocity and remained above that value until peak velocity was attained. Movement endpoint was defined as the first time the velocity decreased below 3% of index fingertip peak velocity and remained under that value for 100 ms.

Performance indices

Since the visuomotor perturbation was applied along each axis of 3D space (triaxial visuomotor perturbation), we examined 3D absolute errors as well as horizontal, sagittal and vertical constant errors. The 3D absolute errors were calculated as the 3D distance in space from the index finger endpoint position to the position of the target. Absolute 3D error values provide a measure of the overall size of endpoint errors made during movement adaptation.

Constant horizontal, sagittal, and vertical errors were computed as the deviation between the coordinates of the target and those of index finger endpoint in the horizontal (lateral direction 'x'), sagittal (radial direction 'y'), and vertical (vertical direction 'z') dimensions. Constant errors (signed errors) were assessed to indicate the spatial location of the hand or bias relative to the target during the learning phase and also importantly during the pre- and post-exposure phases to assess spatial generalization. The visuomotor perturbation shifted the hand trajectory feedback to the right along the horizontal axis, which produced constant horizontal errors of positive signs. By contrast, the sagittal and vertical component of the triaxial perturbation shifted the hand trajectory feedback, respectively, closer and lower from the subject thereby producing negative values of sagittal and vertical constant errors. To represent constant errors made along all three spatial axes on the same scale so that they can be appropriately compared, the signs of constant sagittal and vertical errors were inverted for analyses.

During the first baseline trials, subjects increased their accuracy level and stabilized their performance. For this reason, only spatial errors made during the five last trials of baseline condition were analyzed in this study. Furthermore, to test for changes in trial-to-trial variability by the end of the learning phase, the standard deviation of endpoint errors of each subject over the course of the baseline and the last learning block was computed.

Statistics

To assess learning and generalization of the three-dimensional visuomotor perturbation, data from the different reaching task phases or blocks of trials were subject to separate repeated-measure ANOVAs. For conciseness, only main effects and interactions including the factor phase, block or spatial axis will be reported for all analyses of variance. A significance level of 0.05 was used for all variance analyses performed in this study. Also, Greenhouse–Geisser corrections were applied to all ANOVAs and post-hoc pair-wise comparisons across blocks of trials, task phases or spatial axes were made using a Bonferroni test to reduce the probability of type I error. Finally, effect sizes were computed using the partial eta squared for all ANOVA results.

Results

Learning a triaxial visuomotor perturbation

In the baseline phase, subjects made small and consistent 3D absolute errors across trials (mean 3 cm, SD 0.5 cm; Fig. 3). This indicates that they adequately perceived the target location presented in the VR scene as well as efficiently used their hand trajectory feedback.

Although the size of the visuomotor perturbation increased progressively during the course of the learning phase, the average level of 3D errors displayed only a slight increase relative to the baseline phase level during initial trials of most learning blocks. However, the 3D errors made during the aftereffect trials (mean 9.8 cm) were, on average, three times greater than those made during the baseline condition (3 cm). It is also worth mentioning that the average 3D absolute error made on the first aftereffect trial (mean 12.7 cm) was of similar size to the visuomotor perturbation (13.5 cm). Altogether, these observations indicate that subjects adjusted their movements to the visuomotor perturbation.

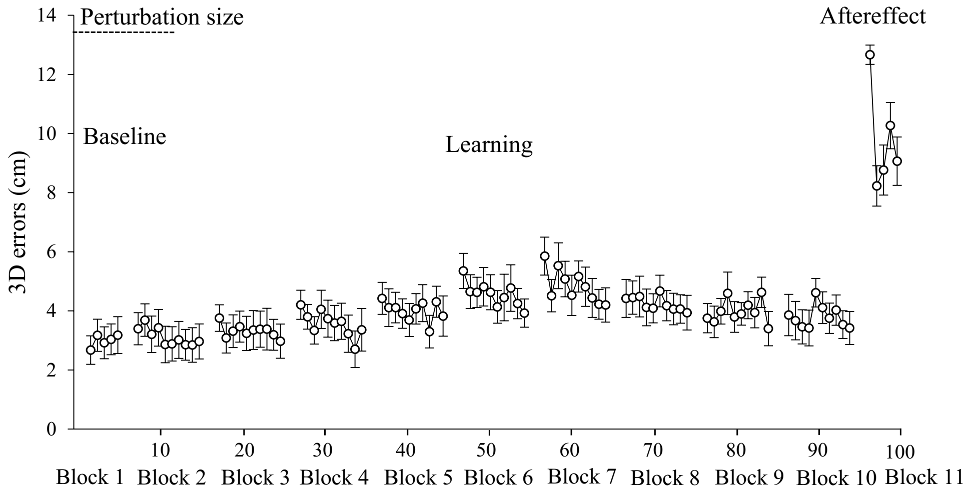

Fig. 3 Mean 3D errors for the baseline, learning, and aftereffect phases. The error bars represent the standard error of the mean

Accordingly, the one-way repeated-measure ANOVA (11 blocks) performed on the 3D absolute errors made during the baseline, learning, and aftereffect trials revealed a main effect of block [$F_{(4.59,59.69)} = 51.17$; $P < 0.05$; 0.79]. Post-hoc analyses indicated that the mean level of 3D errors of only one learning block (block #7) was significantly larger than the magnitude of 3D errors made during baseline trials. Furthermore, the 3D absolute errors made during the aftereffect trials were significantly greater than those made during the baseline as well as all learning blocks ($P < 0.05$).

We further investigated how subjects learn the triaxial visuomotor perturbation by comparing the magnitude of constant errors made during the baseline, learning, and aftereffect trials (Fig. 4). During the baseline trials, horizontal, sagittal, and vertical constant errors were very small and similar. However, differences in the magnitude of constant errors made along each spatial axis arose during initial learning trials and persisted throughout the course of the learning phase. Horizontal and sagittal constant errors tended to decrease over the successive trials of each learning block indicating that subjects efficiently adjusted their movements to the horizontal and sagittal component of the triaxial perturbation. However, this trend was less pronounced for constant vertical errors. Moreover, these learning differences between spatial axes were particularly prominent in the aftereffect trials. The overall average level of constant vertical errors is smaller compared to horizontal and sagittal constant errors, especially during the last aftereffect trials.

Consistent with these observations, the two factors repeated-measure ANOVA (11 blocks × 3 spatial axes) revealed a main effect of block [$F_{(4.33,56.25)} = 130.45$; $P < 0.05$; 0.91], a main effect of axis [$F_{(1.24,16.16)} = 5.16$; $P < 0.05$; 0.28], as well as a block-by-axis interaction [$F_{(3.29,42.73)} = 5.75$; $P < 0.05$; 0.31]. Post-hoc analyses of the main effect of axis did not reach the significance level. However, the block-by-axis interaction indicated several important results. First, there was no difference in the magnitude of constant errors made along the different spatial axes during

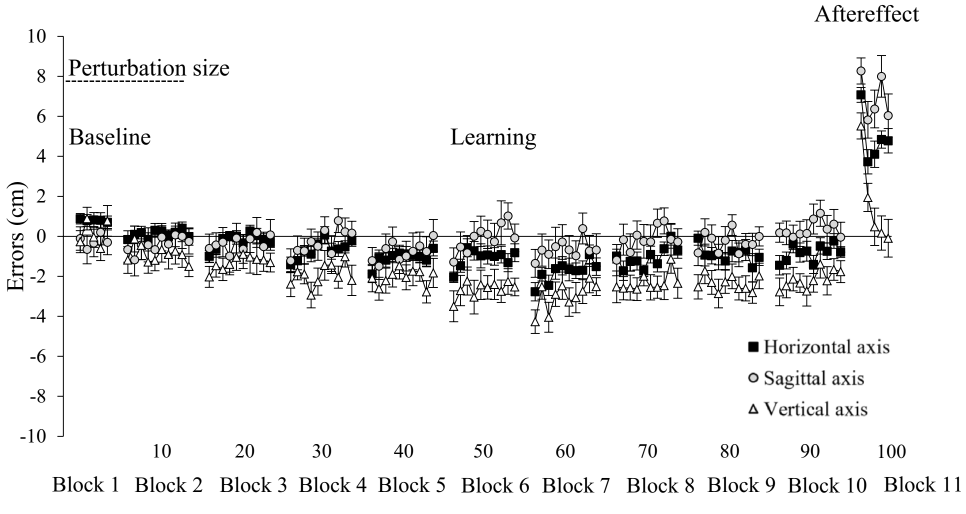

Fig. 4 Mean signed errors for the baseline, adaptation and aftereffect phases for the horizontal, sagittal, and vertical axes. Error bars represent the standard error of the mean

the baseline phase. Second, horizontal and sagittal constant errors were similar during all learning blocks ($P > 0.05$). By contrast, differences were found between vertical and both horizontal and sagittal constant errors during the learning phase. Vertical constant errors were significantly greater than horizontal constant errors for learning block six. Also, vertical constant errors were significantly larger than sagittal constant errors made during learning blocks 9 and 10 ($P < 0.05$). This indicated that during these late learning blocks, when the size of the visual distortion was larger, the less efficient ability of subjects to adapt their movements to the vertical compared to the horizontal and sagittal components of the 3D distortion reached significance. Third, as for the learning phase, constant horizontal and sagittal errors were similar in magnitude during aftereffect trials. However, vertical constant errors were significantly larger than both horizontal and sagittal constant errors during the aftereffect block of trials ($P < 0.05$).

The analysis of intertrial variability between the baseline and the last learning block revealed different trends across the spatial axes. The average level of trial-to-trial variability was smaller along the horizontal axis compared to both the sagittal and vertical axes (Fig. 5). As such, the ANOVA (2 blocks × 3 axes) found a main effect of axis [$F_{(1.56,20.3)} = 11.57$; $P < 0.05$; 0.47]. Post-hoc analyses revealed significant differences between the horizontal axis and both the sagittal and vertical axes ($P < 0.05$). This indicated that subjects produced an overall greater level of intertrial variability, i.e., a more noisy performance along the sagittal and vertical axes compared to the horizontal axis. Furthermore, the ANOVA revealed a marginally significant main effect of block [$F_{(1,13)} = 4.21$; $P = 0.06$; 0.25] and no block-by-axis interaction [$F_{(1.91,24.86)} = 0.88$; $P > 0.05$; 0.063]. Together, the later results suggest that subjects did not fully stabilize their performance along all three spatial axes at the end of the learning session.

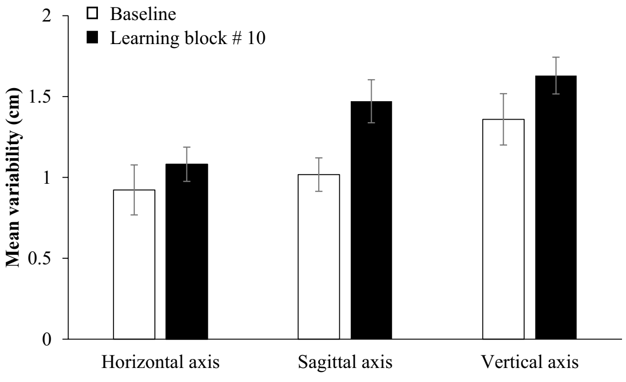

Fig. 5 Mean trial-to-trial variability along the horizontal, sagittal, and vertical axes for the baseline block and the last learning block (block #10). Error bars represent the standard error of the mean

Generalization of visuomotor adaptation

For all six targets and all three spatial axes, the average size of constant errors increased between the pre- and post-exposure phases (Fig. 6). Furthermore, in all cases, this change in errors took place on the opposite side of the visuomotor perturbation. This indicates that subjects applied the recently learned visuomotor association to these novel regions of space, suggesting that spatial generalization occurred.

Spatial generalization of adaptation to the triaxial visuomotor transformation was further analyzed using a three-factor repeated-measure ANOVA (2 phases (pre- and post-exposures) × 3 spatial axes × 6 targets) applied

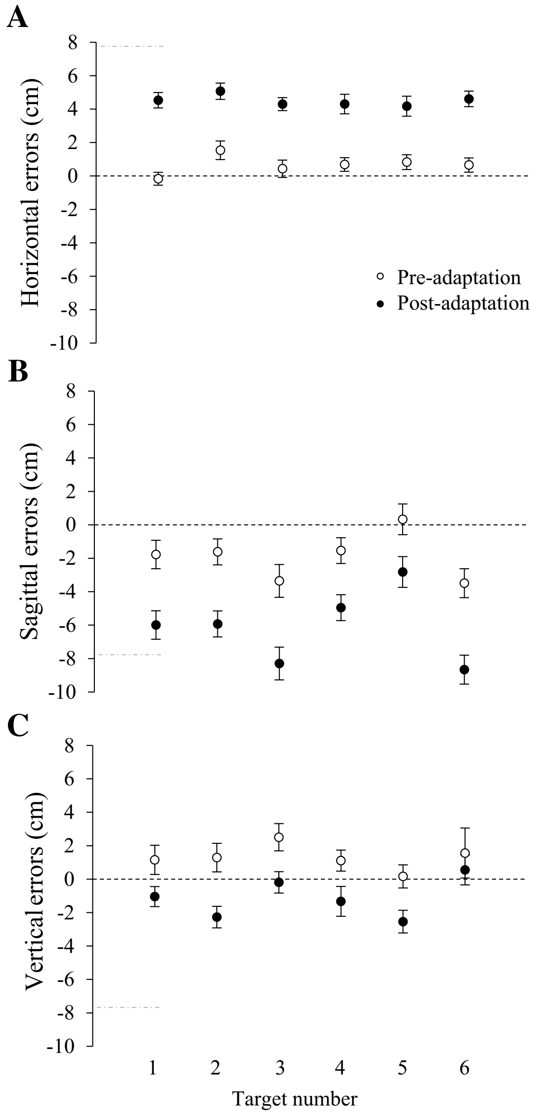

Fig. 6 Mean signed errors made during the generalization test. Pre-adaptation and post-adaptation errors are represented for the horizontal axis (**a**), sagittal axis (**b**) and vertical axis (**c**). The dashed line on the *y*-axis indicates the magnitude of the 3D visuomotor perturbation

on horizontal, sagittal, and vertical constant errors made during the pre- and post-exposure phases. Consistent with the qualitative observations (Fig. 6), the ANOVA showed a main effect of phase [$F_{(1,13)} = 101.11$; $P < 0.05$; 0.88]. Although, the difference between the pre-exposure and post-exposure accuracy level was systematically smaller for the vertical axis than both the horizontal and sagittal axes, the phase-by-axis interaction was only marginally significant [$F_{(1.45,34.5)} = 3.15$; $P = 0.079$; 0.20]. However, the ANOVA revealed a significant phase-by-axis-by-target interaction [$F_{(2.91,34.1)} = 3.26$; $P < 0.05$; 0.20]. Post-hoc tests indicated that the vertical constant errors made while aiming to target six during the pre- and post-exposure phases did not differ ($P > 0.05$). However, for all other targets and component errors, there was a significant difference between the pre- and post-exposure phases ($P < 0.05$).

Discussion

The present study is the first to investigate adaptation and spatial generalization skills using both unconstrained three-dimensional movements and a visuomotor translation perturbation applied along all three axes of 3D space. We used a gradually introduced triaxial translation of the terminal visual feedback of hand trajectory and compared how young adults adapt their movements to the horizontal, sagittal, and vertical components of a triaxial visuomotor perturbation as well as how the newly learned visuomotor association generalizes to novel untrained regions of space.

Visuomotor adaptation to a triaxial perturbation during 3D reaching movements

The results provide evidence that subjects can adjust natural three-dimensional reaches to a gradually increasing translational shift applied simultaneously along the three axes of space. During the learning phase, the mean level of 3D absolute errors made by subjects was generally of similar magnitude to those made during the baseline phase, with only one late learning block showing a higher level of 3D absolute errors than baseline trials. Also, the initial aftereffect trial was, on average, of very similar size to the full visuomotor perturbation and remained much greater than those made during baseline trials in late aftereffect trials. These observations support and extend previous works showing that healthy subjects can adapt three-dimensional reaching movements to translations of the visual feedback (Messier et al. 2007; Mongeon et al. 2013; van den Dobbelsteen et al. 2003).

Visuomotor adaptation skills differed across spatial axes during 3D reaching movements

A major finding of this study was that participants showed spatial axis-dependent visuomotor adaptation capacities. They showed a similar level of spatial accuracy along the horizontal, sagittal, and vertical axes during the baseline phase. In striking contrast, while subjects displayed similar rates of adaptation to the horizontal and sagittal components of the triaxial perturbation, they exhibited a slower adaptation rate as well as a much less persistent adaptation (aftereffect) to the vertical component of the visuomotor perturbation. This finding indicates that subjects were able to adequately plan, control, and adjust their movements along the horizontal, sagittal, and vertical axes during the baseline phase, when there was no adaptation learning requirement. However, when the visuomotor distortion was introduced, subjects faced difficulties in simultaneously compensating for the three components of the triaxial distorsion, which resulted in greater spatial errors along the vertical axis.

How the sensorimotor system adapts three-dimensional reaching movements to various contexts such as change in visual feedback is largely undetermined. Many studies suggested that different movement parameters, such as direction and extent of reaches, may be planned, controlled, and adapted separately by distinct mechanisms (Soechting and Flanders 1989; Gordon et al. 1994; Krakauer et al. 2000; Messier and Kalaska 1997, 1999). In this line, one study found that varying visual feedback conditions during three-dimensional movements differentially altered radial distance, azimuth, and elevation errors suggesting that subjects plan and control motion along all three axes relatively independently (Berkinblit et al. 1995). However, we know very little about how the motor system process spatial errors made along the horizontal, sagittal, and vertical axes to adapt movements to novel visuomotor conditions.

Of particular interest, Ghahramani et al. (1996) used a planar reaching paradigm and compared visuomotor adaptation to a uniaxial translational shift applied either to the horizontal or the sagittal axe in separated experiments. Their results indicated a faster rate of adaptation to the horizontal than the sagittal translational shift of the visual feedback. They suggested that this difference in movement adaptability across spatial axes might be attributed, in part, to biomechanical factors such as anisotropies in the geometry and dynamics of the limb. Our finding that subjects exhibited similar adaptation rates along the horizontal and sagittal axes would appear inconsistent with this prior study. However, there were several methodological differences between the present study and the task paradigm of Ghahramani et al. (1996).

Notably, in the present study, subjects were required to simultaneously adapt their movements to a triaxial translational shift of the visual feedback while controlling a greater number of degrees of freedom as well as compensating for the complex interactions between inertial and gravitational forces. Therefore, the combination of complexities arising both from the requirements to learn a novel multiaxial visuomotor association and the biomechanical demands of three-dimensional reaching movements likely impacted on the planning and adaptation mechanisms in this study. Nevertheless, both the overall greater intertrial variability level along the sagittal and vertical axes compared to the horizontal axis as well as the slower adaptation learning rate along the vertical axis relative to the horizontal and sagittal axes are consistent with the general idea that separated independent planning and adaptation mechanisms may take place along the horizontal, sagittal, and vertical axes.

Furthermore, it is worth mentioning that in the two previous studies that examined adaptation of three-dimensional movements using either a biaxial (horizontal and vertical) or a triaxial translational visuomotor perturbation, subjects displayed a slower mean rate of movement adaptation along the vertical axis (Messier et al. 2007; Mongeon et al. 2013). Our results support and extend these previous findings and suggest that adapting three-dimensional movements along the vertical axis represent a greater challenge for the sensorimotor system than movement adaptation along the horizontal and sagittal axes.

Previous studies indicated that vision and proprioception contribute differentially to different aspects of arm movement planning in the horizontal plane (Sober and Sabes 2003; Sainburg et al. 2003). Of relevance, evidence suggests that movement planning along the vertical axis may rely on processes involving vision and proprioception that differ from movements performed in the horizontal plane. Since proprioceptive signals have been suggested to play a critical role in anticipating arm configuration-dependent effects of gravity (Proske 2005), one might propose that proprioception is more important than vision for movement planning in the vertical plane. Apker et al. (2011) addressed this question using a protocol in which visual and somatosensory cues about limb position were dissociated either along the horizontal or the vertical axis prior to movement onset. Their findings suggested that vision and proprioception contribute equally to arm movement planning in the vertical plane when the dissociation was applied along the horizontal axis. By contrast, proprioception contributed more strongly in movement planning when vision and proprioception were dissociated along the vertical axis. Our results are compatible with these findings.

Of particular interest, another recent study by Toma et al. (2015) used an elegant visuomotor paradigm in which horizontal movements were perceived as vertical. Participants rapidly corrected for the spatial errors induced by the large visuomotor perturbation. However, they progressively adopted a suboptimal motion, i.e., a velocity profile close to that of vertical movements. Authors argued that the higher weight given to distorted visual feedback in their study may result from the continuous and predictable effect of the gravitational force field on the body.

In this perspective, our findings of less efficient adaptation and much smaller aftereffect measured along the vertical axis suggest that the motor plan did not rely more on the visually perceived vertical position of the hand, but rather appears to depend more strongly on the constant mechanical effect of gravity sensed using proprioceptive and vestibular signals. In the current experiment, we manipulated visual feedback while proprioceptive and vestibular information remained congruent and relevant with respect to gravity. Therefore, it is plausible that, in the context of a visual distortion, the robust internal representation of gravity we develop while interacting with gravito-inertial forces in daily life reduces our ability to rapidly learn a novel visuo-proprioceptive association along the vertical axis. This is consistent with the idea that earth gravity is a strong prior (Jörges and López-Moliner 2017). Such robust internal model of gravity might benefit the performance of highly skilled athletes while resisting to potential visual illusions (e.g., acrobat skier).

We suggest that the slower rate of adaptation and the reduced aftereffect seen along the vertical axis compared to the horizontal and sagittal axes reflects the higher weight given to proprioception when adjusting movements along the vertical axis. In this perspective, we propose that efficient proprioceptively based visuomotor adaptation requires more learning trials than visually based adaptation. That is, when the demand for proprioceptive processing is higher, such as when adapting movement along the vertical axis, the number of trials required to reach asymptotic performance is greater. This hypothesis is consistent with the frequently reported observation that adapting planar movements to a novel force field, which is considered to depend more greatly on proprioceptive processing, presents a slower time course than visuomotor adaptation (Krakauer et al. 1999).

This sensory channel specialisation hypothesis for movement planning and adaptation across spatial axes is consistent with a modular decomposition strategy to visuomotor adaptation (Ghahramani and Wolpert 1997). According to this scheme, participants may have simplified the complex multiaxial adaptive problem by learning separate visuomotor maps according to the unique visuo-proprioceptive demands of moving along each spatial axis. In this view, it is possible that the motor system prioritized adaptation along the horizontal and sagittal axes because such adaptation depends on more similar visuo-proprioceptive requirements compared to adaptive updating along the vertical axis which likely involves both a more profound reweighting process between vision and proprioception and the integration of vestibular inputs (Le Seac'h and McIntyre 2007; Mars et al. 2003). Future studies comparing proprioceptively based and visually based visuomotor adaptation in the context of single and multiaxial visuomotor perturbations are required to elucidate these questions. Other future studies performed in virtual reality might assess whether awareness of the virtual distortion and more extensive training improve movement adaptation along the vertical axis.

Visuomotor adaptation to a triaxial perturbation generalizes to novel spatial regions

We assessed, for the first time, the spatial generalization of a gradually introduced triaxial perturbation in a 3D virtual environment. While remaining unaware of the large visuo-proprioceptive discrepancy, subjects were able to generalize the novel visuomotor association to untrained regions of the workspace. As for the learning phase, the average level of spatial generalization was systematically smaller along the vertical than along the horizontal and sagittal axes. However, this between-axis difference in spatial generalization reached significance for only one target.

Studies of spatial generalization have used a wide array of experimental paradigms. Several factors related to the reaching task features and training conditions seem to account for the differences in the magnitude of spatial generalization across studies (Ghahramani et al. 1996; Vetter et al. 1999; Pearson et al. 2010; Taylor and Ivry 2013; Bédard and Song 2013). The single study (Vetter et al. 1999) assessing spatial generalization in three-dimensional space used an experimental paradigm that differed from our protocol in several important respects. First, their study involved a translation shift of the visual feedback applied along a single axis (horizontal) of 3D space. Simultaneously processing spatial errors along the horizontal, sagittal and vertical axes to adapt movements to a triaxial visuomotor perturbation might represent a greater challenge for the motor system. Second, while we did not use any refresher visual feedback, Vetter et al. (1999) provided such feedback every three trials. Frequent reminder of the newly learned visuomotor association is used to prevent decay of learning and may enhance spatial generalization. Third, in their paradigm, the perturbation size was consistently smaller than in the present study. It has been suggested that perturbation size influences the stability of adaptation (Krakauer et al. 2005; Ruttle et al. 2016; Joiner et al. 2013). Although, our results do not allow dissociating the impact of these factors, they all likely contributed to the observed apparent smaller generalization magnitude in the present study compared to Vetter et al. (1999). Nevertheless, the overall significant changes in pointing behavior between the pre- and post-exposure phases support and extend their main conclusion that the motor system can broadly generalize visuomotor adaptation of three-dimensional movements even when using a single learning target, i.e., when subjects are exposed to a highly localized visuomotor remapping.

Ghahramani et al. (1996) reported larger adaptive changes following adaptation to shifts in the horizontal axis compared to the sagittal axis, which was reflected in the following generalization. In contrast, the difference in the magnitude of spatial generalization across spatial axes reached significance for only one target along the vertical axis in this study. While this result appears inconsistent with the markedly smaller learning effect found along the vertical axis, the large variability measured along the vertical axis during all experimental phases and especially during the generalization test likely produced a shortfall in statistical power. Reaching to visual target in the three-dimensional workspace generally increases endpoint variability compared to planar movements. In the present study, additional variability might also have resulted both from the attempt to simultaneously compensate for spatial errors introduced along each spatial axis over successive blocks of trials during the learning phase and also possibly from the gradual decay of learning during the generalization phase.

It is also plausible that the distance between the training and the generalization target explains, in part, the magnitude of generalization in the present study. Previous studies found a decaying pattern of generalization as distance between the learning and generalization targets increases (Ghahramani et al. 1996; Mattar and Ostry 2007). Our study does not allow us to assess this possibility since all generalization targets were equidistant from the learning target along the horizontal, sagittal, and vertical axes. Furthermore, as the distance between the learning and generalization targets was relatively small in the current study (8 cm along the horizontal, sagittal and vertical axes), it is undetermined whether the broad generalization we observed would be maintained for targets located at a more distant location. Future studies of three-dimensional movements varying the nature and the size of the visuomotor perturbation as well as the spatial arrangements of the generalization targets are needed to better understand the process of visuomotor learning during natural unconstrained movements.

In conclusion, our exploratory study supports the idea that adapting three-dimensional movements might involve distinct processes according to the specific sensorimotor integration requirements of moving along each spatial axis. Furthermore, our findings indicated that the learning of a novel triaxial visuomotor association is not limited to the area of training. The superior parietal lobule might play a significant role in such adaptive mechanisms as neurons in these regions displayed neural tuning along the distance, azimuth, and elevation axes (Lacquaniti et al. 1995). Basal ganglia might also represent a neural substrate of such complex adaptive behavior given both its contribution to sensorimotor learning and its modular organization (Graybiel et al. 1994). Understanding the plasticity of the visuomotor system in situations that simulate the challenges of daily adaptations is crucial if we seek to elucidate processes underlying everyday motor actions, athletic performances or rehabilitation of movement disorders.

Acknowledgements This work was supported by the Fondation du Grand défi Pierre Lavoie, Quebec, Canada. We wish to thank Marcel Beaulieu, the engineer who provided expert technical assistance, as well as David Mongeon and Stéphanie Bergeron who helped us throughout this experiment.

References

Apker GA, Karimi CP, Buneo CA (2011) Contributions of vision and proprioception to arm movement planning in the vertical plane. Neurosci Lett 503(3):186–190

Bédard P, Song JH (2013) Attention modulates generalization of visuomotor adaptation. J Vision 13(12):12

Berkinblit MB, Fookson OI, Smetanin B, Adamovich SV, Poizner H (1995) The interaction of visual and proprioceptive inputs in pointing to actual and remembered targets. Exp Brain Res 107(2):326–330

Desmurget M, Jordan M, Prablanc C, Jeannerod M (1997) Constrained and unconstrained movements involve different control strategies. J Neurophysiol 77(3):1644–1650

Ghahramani Z, Wolpert DM (1997) Modular decomposition in visuomotor learning. Nature 386(6623):392–395

Ghahramani Z, Wolpert DM, Jordan MI (1996) Generalization to local remappings of the visuomotor coordinate transformation. J Neurosci 16(21):7085–7096

Gordon J, Ghilardi MF, Cooper SE, Ghez C (1994) Accuracy of planar reaching movements. II. Systematic extent errors resulting from inertial anisotropy. Exp Brain Res 99(1):112–130

Graybiel AM, Aosaki T, Flaherty AW, Kimura M (1994) The basal ganglia and adaptive motor control. Science 265(5180):1826–1831

Heuer H, Sülzenbrück S (2012) A progression of approximations to internal models of complex visuo-motor transformations. Hum Mov Sci 31:1056–1070

Joiner WM, Brayanov JB, Smith MA (2013) The training schedule affects the stability, not the magnitude, of the interlimb transfer of learned dynamics. J Neurophysiol 110(4):984–998

Jörges B, López-Moliner J (2017) Gravity as a strong prior: implications for perception and action. Front Hum Neurosci 11:203

Kagerer FA, Contreras-Vidal JL, Stelmach GE (1997) Adaptation to gradual as compared with sudden visuo-motor distortions. Exp Brain Res 115(3):557–556

Kluzik J, Diedrichsen J, Shadmehr R, Bastian AJ (2008) Reach adaptation: what determines whether we learn an internal model of the tool or adapt the model of our arm? J Neurophysiol 100(3):1455–1464

Krakauer JW, Ghilardi MF, Ghez C (1999) Independent learning of internal models for kinematic and dynamic control of reaching. Nat Neurosci 2(11):1026–1031

Krakauer JW, Pine ZM, Ghilardi MF, Ghez C (2000) Learning of visuomotor transformations for vectorial planning of reaching trajectories. J Neurosci 20(23):8916–8924

Krakauer JW, Ghez C, Ghilardi MF (2005) Adaptation to visuomotor transformations: consolidation, interference, and forgetting. J Neurosci 25(2):473–478

Lacquaniti F, Guigon E, Bianchi L, Ferraina S, Caminiti R (1995) Representing spatial information for limb movement: role of area 5 in the monkey. Cereb Cortex 5(5):391–409

Le Seac'h AB, McIntyre J (2007) Multimodal reference frame for the planning of vertical arms movements. Neurosci Lett 423(3):211–215

Mars F, Archambault PS, Feldman AG (2003) Vestibular contribution to combined arm and trunk motion. Exp Brain Res 150:515–519

Mattar AAG, Ostry DJ (2007) Modifiability of generalization in dynamics learning. J Neurophysiol 98(6):3321–3329

Messier J, Kalaska JF (1997) Differential effect of task conditions on errors of direction and extent of reaching movements. Exp Brain Res 115(3):469–478

Messier J, Kalaska JF (1999) Comparison of variability of initial kinematics and endpoints of reaching movements. Exp Brain Res 125:139–152

Messier J, Adamovich S, Jack D, Hening W, Sage J, Poizner H (2007) Visuomotor learning in immersive 3D virtual reality in Parkinson's disease and in aging. Exp Brain Res 179(3):457–474

Michel C, Pisella L, Prablanc C, Rode G, Rossetti Y (2007) Enhancing visuomotor adaptation by reducing error signals: single-step (aware) versus multiple-step (unaware) exposure to wedge prisms. J Cogn Neurosci 19(2):341–350

Mongeon D, Blanchet P, Messier J (2013) Impact of Parkinson's disease and dopaminergic medication on adaptation to explicit and implicit visuomotor perturbations. Brain Cogn 81(2):271–282. https://doi.org/10.1016/j.bandc.2012.12.001

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9(1):97–113

Pearson TS, Krakauer JW, Mazzoni P (2010) Learning not to generalize: modular adaptation of visuomotor gain. J Neurophysiol 103(6):2938–2952

Proske U (2005) What is the role of muscle receptors in proprioception? Muscle Nerve 31:780–787

Ruttle JE, Cressman EK, Marius't Hart B, Henriques DY (2016) Time course of reach adaptation and proprioceptive recalibration during visuomotor learning. PLoS One. 11(10):e0163695

Saijo N, Gomi H (2010) Multiple motor learning strategies in visuomotor rotation. PLoS One 5(2):e9399

Sainburg RL, Lateiner JE, Latash ML, Bagesteiro LB (2003) Effects of altering initial position on movement direction and extent. J Neurophysiol 89:401–415

Shabbott BA, Sainburg RL (2010) Learning a visuomotor rotation: simultaneous visual and proprioceptive information is crucial for visuomotor remapping. Exp Brain Res 203(1):75–87

Sober SJ, Sabes PN (2003) Multisensory integration during motor planning. J Neurosci 23(18):6982–6992

Soechting JF, Flanders M (1989) Sensorimotor representations for pointing to targets in three-dimensional space. J Neurophysiol 62(2):582–594

Taylor JA, Ivry RB (2013) Context-dependent generalization. Front Hum Neurosci. https://doi.org/10.3389/fnhum.2013.00171

Toma S, Sciutti A, Papaxanthis C, Pozzo T (2015) Visuomotor adaptation to a visual rotation is gravity dependent. J Neurophysiol 113(6):1885–1895

van den Dobbelsteen JJ, Brenner E, Smeets JB (2003) Adaptation of movement endpoints to perturbations of visual feedback. Exp Brain Res 148(4):471–481. https://doi.org/10.1007/s00221-002-1321-4

Vetter P, Goodbody SJ, Wolpert DM (1999) Evidence for an eye-centered spherical representation of the visuomotor map. J Neurophysiol 81(2):935–939