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Prism adaptation in virtual and natural contexts: Evidence for a flexible adaptive process

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1

Abstract

Prism exposure when aiming at a visual target in a virtual condition (e.g., when the hand is represented by a video representation) produces no or only small adaptations (aftereffects), whereas prism exposure in a natural condition produces large aftereffects. Some researchers suggested that this difference may arise from distinct adaptive processes, but other studies suggested a unique process. The present study reconciled these conflicting interpretations. Forty participants were divided into two groups: one group used visual feedback of their hand (natural context), and the other group used computer-generated representational feedback (virtual context). Visual feedback during adaptation was concurrent or terminal. All participants underwent laterally displacing prism perturbation. The results showed that the aftereffects were twice as large in the 'natural context' compared to the 'virtual context'. No significant differences were observed between the concurrent and terminal feedback conditions. The aftereffects generalised to untested targets and workspace. These results suggest that prism adaptation in virtual and natural contexts involves the same process. The smaller aftereffects in the virtual context suggest that the depth of adaptation is a function of the degree of convergence between the proprioceptive and visual information that arises from the hand.

Key words: prism adaptation, object unity assumption, realignment and recalibration, virtual and natural contexts, aftereffects

2

Introduction

Adaptive processes to new environments were studied for many years by the introduction of visuomotor perturbations using prismatic lenses (Helmholtz, 1909/1962). These lenses produce a lateral displacement of the entire visual field (e.g., 10 degrees to the right), but incoming information from the remaining senses remains intact. The movement endpoint of the first few attempts to perform goal-directed movements in this new context is biased in the direction of the prism-induced visual perturbation. An individual adapts to the visual perturbation after only a few practice trials, and the endpoint accuracy/variability of goal-directed movements returns to pre-exposure levels. The participant adapts to this new visuomotor context. How did the participant succeed?

Prism adaptation involves two distinct processes: realignment and recalibration, as termed by Redding and Wallace (2002, 2006), or sensory recalibration and visuomotor skill acquisition as termed by Clower and Boussaoud (2000). One simple example of these two processes occurs when the telescopic sight of a rifleman is misaligned 10° to the right (Newport & Jackson, 2006). A rifleman realises that the shots are hitting to the right of the target after a few shots, and he can either shoot 10 degrees to the left (analogous to the recalibration process) or adjust the sight of his rifle until it is properly aligned (analogous to the realignment process).

The above example suggests that recalibration is a cognitive process that involves strategies such as side-pointing (i.e., deliberately planning one's movement in the direction opposite to the prismatic displacement) or online corrections to the movement trajectory (Newport & Jackson, 2006). Removal of the perturbation produces an aftereffect: the movement now ends in the direction opposite to prismatic displacement. Recalibration occurs rapidly after the introduction of a perturbation, sometimes within a few trials, but the ensuing aftereffect is specific to the workspace and targets submitted to the perturbation (Clower & Boussaoud, 2000; Redding & Wallace, 2006). However, realignment is a sensory process that results in a slow and gradual tuning (re-correlation) of visual and proprioceptive spatial maps. Therefore,

3

adaptation for the prismatic displacement of the visual field generalises to the complete workspace (Clower & Boussaoud, 2000; Newport & Jackson, 2006; Redding & Wallace, 2006).

The presence of these two distinct, although not exclusive, processes is supported by neuroimaging studies in the intact brain. In their seminal work, Clower et al. (1996) measured changes in regional cerebral blood flow (rCBF) that were associated with pointing movements under the influence of laterally displacing prisms. These investigators reversed the orientation of the prism wedge every five trials to force participants to continuously correct their movements for the prism-induced bias. This condition is associated with error correction during prism adaptation, and it triggered activation of the contralateral intraparietal sulcus (IPS). Therefore, these results support a role of the posterior parietal cortex in the recalibration process (Clower et al., 1996; Danckert, Ferber, & Goodale, 2008; Luaute et al., 2009). Similarly, Luauté et al. (2009) performed a trial-by-trial analysis that revealed activation of the contralateral anterior intraparietal sulcus (aIPS) soon after the introduction of a prism that was directly proportional to the prism-induced pointing error; the error and aIPS activation decreased with successive trials. This result suggests an important role for the aIPS in error detection. In contrast, a reduction in prism-induced error was coupled with a larger activation of the contralateral parieto-occipital sulcus (POS), which suggests an important role for this area in error correction. The results of Luauté et al. also revealed a larger activation of lobules IV and V in the ipsilateral cerebellum soon after prism introduction. Specifically, a trial-by trial analysis revealed that activation of these lobules increased progressively during the early phase of prism exposure, and activation remained high even after initial improvements in pointing accuracy. Therefore, the posterior parietal cortex appears largely involved in the recalibration process that results from prism introduction, and the cerebellum is largely involved in the realignment process of visual and sensorimotor spatial maps (but see also Chapman et al., 2010).

Redding and Wallace (2006) demonstrated that realignment only occurs if the participant becomes aware of a misalignment between proprioceptive and visual maps (however see Michel, Pisella, Prablanc, Rode, & Rossetti, 2007). Moreover, realignment only occurs when information arising from the different

4

senses (vision and proprioception) are perceived as a single multisensory event ("I feel what I see"; the seen and felt position of the hand are congruent) rather than two separate unimodal events (the seen and felt position of the hand are incongruent), which is the so-called 'object unity assumption' (Bedford, 1993; Redding & Wallace, 2006; Welch & Warren, 1980). These observations raise an important question. Can realignment occur in virtual reality settings in which the sensed and seen location of the hand do not match, which violates the object-unity assumption (Redding and Wallace, 2006)? Specifically, visual and proprioceptive feedback do not arise from a single origin (a cursor shown on a screen and proprioceptive feedback from the arm) as it does in natural settings (one's hand and proprioceptive feedback from the arm). Therefore, adaptation may only result from a recalibration process in virtual reality settings (Redding & Wallace, 2006).

For example, Clower and Boussaoud (2000) had participants perform goal-directed movements under a condition of perfect spatial correspondence between visual and the proprioceptive feedback of the hand ('actual condition'); a LED light was affixed on a participant's fingertip. In a 'representational condition', a spatial discrepancy was introduced between these two sensory signals; the hand was represented by a cursor on the computer screen. Participants in both conditions adapted similarly to a prismatic displacement of visual information, but significant aftereffects were observed only after exposure to the 'actual condition'. This result led Clower and Boussaoud (2000) to conclude that the noted aftereffects for the actual condition resulted from a realignment process (perceptual recalibration), but the absence of an aftereffect in the 'representational condition', reflected the contribution of a recalibration process (visuomotor skill acquisition) (however see:Goodbody & Wolpert, 1999).

In another prismatic adaptation study, Norris et al. (2001) had participants perform goal-directed movements in one of three conditions: participants in the 'natural context' condition could see their hand; participants in the 'video-context' condition could see their hand progressing toward the target but via a 'real-time video' that was presented on a vertical computer screen; and participants in the 'virtual-context' condition could not see their hand but a cursor representing the participant's hand was displayed

5

on a vertical computer screen. Withdrawal of the visual perturbation after the adaptation phase resulted in significant aftereffects for the three conditions. This aftereffect became larger as the task became more natural (natural > video > virtual). Norris et al. interpreted their findings to indicate the occurrence of a common adaptation process in all three tasks.

The goal of the present study is to reconcile these conflicting interpretations and determine whether recalibration, realignment or both processes occur during reactions to a prismatic perturbation in a virtual context. More specifically, we tested the hypothesis that no realignment would occur in a virtual aiming task because the conditions of object unity assumption are not met. However, different levels of the lacking of object unity are possible in a virtual reality context. For example, this lack of unity is smaller in a video aiming task when the task is performed with concurrent visual feedback than when only terminal visual feedback is available. This difference occurs because online/concurrent visual information is typically more important for movement control than other sources of sensory information. Therefore, the lack of unity might be more difficult to detect. However, proprioception becomes more important for movement control when concurrent visual feedback is not available. Therefore, the discrepancy between the felt position of one's hand and the seen position of the cursor becomes more evident in a terminal feedback condition in which visual feedback only becomes available late in the movement. We determined whether the hypothesised lack of realignment was more evident when only terminal visual feedback was available during adaptation.

An experimental protocol developed by Redding and Wallace (2006) was used to reach our goal. Participants performed a virtual task or a natural task. Each task was performed with either concurrent or terminal visual feedback during the adaptation phase (see below). Vision of the hand in the virtual task was represented by a cursor on a computer screen. Vision of the hand in the natural task was directly available to the participant. Participants underwent two pre/post-tests and one adaptation phase. Participants wore 20-dioptres prism lenses (base left) during the adaptation phase, and they wore neutral lenses in the pre/post-tests. As mentioned previously, the recalibration process does not produce

6

aftereffects or produces only small amounts of aftereffects. Additionally, reported recalibration aftereffects are specific to the conditions in which the perturbation occurred. Therefore, participants performed one pre/post-test task under the same condition as the adaptation phase (same initial arm configuration and towards the same visual target) to measure the contribution of this process to adaptation. We also introduced two test targets that were not visually perturbed to measure the generalisation of the recalibration process. These targets were located five degrees to the right and left of the adapted target. Larger aftereffects were expected for the adapted target than the two test targets, which should not differ significantly from each other (Redding and Wallace, 2006).

The realignment process generalised to untrained regions and workspaces. Therefore, participants underwent another pre/post-test in which their initial arm configuration differed from the recalibration test and adaptation phase to measure the contribution of this process. Two test targets were positioned five degrees to the right and left of the adapted target. We expected similar aftereffects across all three targets because realignment generalises linearly (Redding and Wallace, 2006).

We should observe aftereffects for the recalibration, but not the realignment, test when the virtual context does not meet the required conditions defined by the object unity assumption because this assumption must be met to detect a misalignment. The difference between the aftereffects should be larger for the terminal than the concurrent visual feedback condition. Moreover, we were expecting smaller recalibration aftereffects for the virtual task than the natural task condition (Norris et al., 2001; Clower and Boussaoud, 2000).

Methods

Participants

Forty undergraduate students were recruited in the Département de Kinésiologie from the Université de Montréal. Participants had no previous experience with the experimental task. All

7

participants reported normal or corrected-to-normal vision. The Health Sciences Ethics Committee of the

Université de Montréal approved this study.

Task and apparatus (see Figure 1)

Participants performed a manual aiming task in which they moved a computer mouse-like device

on a horizontal surface from a fixed starting position towards one of three possible targets. The apparatus

consisted of a computer screen, a table, a two-degrees of freedom manipulandum, and a starting base. The

computer screen (Mitsubishi, Color Pro Diamond 37 inches; 60 Hz refresh rate) was mounted on a ceiling

support positioned directly over the table, and it was oriented parallel to the table surface. Images were

reflected on a semi-reflecting mirror placed directly beneath the screen and parallel to the tabletop. The

distance between the computer screen and the mirror was 23 cm, and the distance between the mirror and

tabletop was 23 cm during the recalibration pre/post-tests and exposure phase. The distance between the

computer screen and the mirror was 35 cm during the realignment pre/post-tests (see the procedure

section for more details). This configuration allowed free displacement of the manipulandum on the

tabletop.

A piece of Plexiglas covered the tabletop, and a starting base and manipulandum were affixed to

the surface. The starting base consisted of a thin strip of Plexiglas glued to the tabletop that was parallel to

the leading edge of the table with a small indentation on one side. This indentation was located directly

parallel with the lateral centre of the computer screen and the participant's midline. This indentation eased

participant's positioning of the stylus on the starting base at the beginning of each trial.

The manipulandum consisted of two pieces of rigid Plexiglas (43 cm) joined together at one end by

an axle. One free end of the manipulandum was fitted with a second axle that was encased in a stationary

base. The other free end of the manipulandum was fitted with a small aluminium vertical shaft (length: 5

cm, radius: 3 mm). Therefore, the stylus could be easily gripped by the participant. From the participants'

perspective, the far end of the manipulandum was located 40 cm to the left of the starting base and 70 cm

8

in the sagittal plane. Each axle of the manipulandum was equipped with a 13-bit optical shaft encoder (U.S. Digital, Vancouver, WA, USA, model S2-2048, sampled at 500 Hz, angular accuracy of 0.0439°), which allowed us to track the displacement of the stylus online and illustrate it using a 1:1 ratio on the computer screen. The bottom of the stylus and the bottom of the optical encoder were located at the junction of the two arms of the manipulandum and covered with a thin piece of Plexiglas. Lubrication of the working surface at the beginning of each experimental session ensured a near frictionless displacement of the stylus.

<u>Experimental conditions</u>

Participants were randomly assigned to one of four experimental groups. These groups (n = 10 for each group) were differentiated by the context in which the task was performed (natural context or virtual context) and the visual feedback condition (concurrent or a terminal visual feedback condition).

The hands of participants in the virtual context condition were represented by a cursor on a computer screen (red, radius: 3 mm). Displacement of the manipulandum in this situation was represented on a computer screen by the real time displacement of the cursor at a 1:1 ratio. The experimenter asked participants to reach a target that was presented on the computer screen (white, radius: 4 mm) using the cursor. The semi-reflecting mirror located between the computer screen and tabletop prevented participants from seeing their hand.

The hands of participants in the natural context condition were directly visible. Visualisation was performed via illumination of that portion of the workspace between the tabletop and the semi-reflecting mirror using white LED lights beneath the mirror. Activation of the LEDs was controlled through a computer program (see the visual feedback condition for more details), which allowed us to control hand visibility during different portions of the movement with negligible delays (50 ms). A round sticker (white, radius: 3 mm) was affixed to the top of the stylus, which played the same role as the cursor in the

9

virtual context condition. The experimenter asked participants to reach a target that was presented on a computer screen (white, radius: 4 mm) using the stylus.

In all context and visual feedback conditions, the visual information that was related to the effector (the cursor or hand) was never visible while the hand rested on the starting base and after movement completion when the effector returned to the starting base. Only the visual target was visible during the entire trial (Redding & Wallace, 2006). Vision of the effector in the terminal vision condition was permitted at 27 cm from the starting base (i.e., the last 10% of the distance between the starting base and the visual target (Redding & Wallace, 2006)) and up to the cursor/stylus endpoint. Vision of the effector in the concurrent vision condition was allowed from movement onset to movement completion, or during 100% of movement amplitude.

Procedure

Participants underwent three experimental phases (pre-tests, adaptation and post-tests). The pre/post-tests were the same for all experimental groups, and these tests were performed in a no vision/no knowledge of result condition, i.e., no visual information related to the starting base, the cursor or the hand was available prior to, during and after movement completion. Participants wore plastic glasses mounted with neutral lenses during these tests, which were similar to the glasses mounted with the prism lenses that were used during the exposure phase.

The pre-test phase allowed us to determine the baseline performance of each participant, which was then compared to his/her post-test performance to detect the presence of any aftereffects. Pre/post-tests were divided into two distinct tests, a recalibration test and a realignment test. It has been suggested that the realignment process generalises to unexposed conditions and workspaces, but recalibration is specific to the exposure condition. Therefore, the realignment test was performed in a different workspace than the recalibration test and the exposure phase; it was located 12 centimetres below the position in the recalibration test and the exposure phase (Redding & Wallace, 2006). This positioning resulted in the

10

participant having to initiate his/her movement using a different arm configuration than the recalibration

test and the exposure phase (Redding & Wallace, 2006). In addition to the exposure target (located 30 cm

straight ahead on the participant's sagittal midline), two 'test' targets located 5 degrees to the right and

left of the exposure target were also used in this phase.

Participants in the realignment test performed ten pointing movements without visual feedback of

the effector toward each of the three targets at -5°, 0°, and 5° relative to the participant's midline and

starting base. Targets were presented in a random order. Participants were asked to try to complete their

movements in 830 ms (36 cm/s; Redding & Wallace, 2009). This test provides a measure of the

aftereffects of the realignment process.

Participants performed the recalibration test following the realignment test. This test was identical

to the total realignment test described above, with the exception that the starting position and the

workspace were located 12 cm above the realignment test. This position of the working surface was

maintained during the exposure phase. This test provides a measure of the aftereffects of the recalibration

process (Redding & Wallace, 2006).

The neutral glasses were removed after the realignment and recalibration pre-tests and replaced

by glasses mounted with 20 dioptre Fresnel prismatic lenses (base left; Cotter, 2002) that laterally

displaced the visual field 11.4° to the right. Participants were informed that a perturbation was introduced

for this exposure phase, but they were not informed of its nature. Participants pointed towards the

exposure target (0°) 50 times. Participants initiated their movements as they pleased (not a reaction time

task), and they were asked to reach the target as accurately as possible in a movement time of 830 ms.

Participants were allowed to see the target and the effector (hand or cursor) for approximately 500 ms

after movement completion, which provided knowledge of the result.

The prismatic lenses were removed after the exposure phase was completed and replaced by

neutral lenses for the post-tests. All participants completed the recalibration post-test (Redding &

11

Wallace, 2006) prior to the realignment post-test. Each test was similar to the pre-tests in all respects. An average delay of two minutes occurred between the end of the exposure phase and the post-tests.

<u>Data analysis</u>

Movement endpoint

The direction error is the signed difference on the front axis (in mm) between the movement endpoint and the target. A positive value indicates a movement that ended to the right of the target, and a negative value indicates a movement that ended to the left of the target. We computed constant (signed) and variable (within participant variability) aiming errors for the direction dimension of the task.

Kinematic data

Movement initiation was defined as the moment at which tangential velocity of the stylus reached 10 mm/s, and movement was deemed completed when the stylus was not displaced by more than 2 mm in a time frame of 50 ms. This procedure ensured that the participants did not produce corrective submovements (Redding & Wallace, 2006; Veilleux & Proteau, 2011a, 2011b).

The tangential displacement data of the stylus over time were first smoothed using a second order recursive Butterworth filter with a cutting frequency of 10 Hz. The filtered data were then numerically differentiated once using a central finite technique to obtain the velocity profile of the aiming movement, a second time to obtain the acceleration profile, and a third time to obtain a jerk profile. We determined the moment and location of occurrence (in Cartesian coordinates) of peak acceleration, velocity and deceleration of the movement's primary impulse from these profiles.

Statistical analyses

Details of dependent variables of interest, the rationale for their use, and the statistical analyses that were computed are defined at the beginning of each results subsection to facilitate the reading of this article. Geisser-Greenhouse correction was applied when Epsilon was smaller than 1. Significant interactions were broken down by computing simple main effects, which were followed by post hoc

comparisons (Dunn's technique) when they involved more than two mean values. All effects are reported at $p < .05$ (adjusted for the number of comparisons using Bonferroni).

Results

<u>Exposure phase</u>

First, we performed an analysis to determine whether participants in different experimental groups adapted differently to prism perturbation. We computed independent ANOVAs for the direction constant error and direction variable error to contrast the 2 contexts (Virtual and Natural) x 2 visual feedback conditions (Concurrent and Terminal) x 10 blocks of trials (1-5, 6-10, ..., 46-50), using repeated measurements on the last factor.

Movement endpoint

Direction constant and variable error (Figure 2 and Tables 1 and 2)

(Table 1 about here)

ANOVA for the direction constant error (Table 1) revealed a significant Visual feedback x Block interaction, $F(9, 324) = 13.33$, $p < 0.001$. The direction constant error for the first block of trials was significantly larger in the Terminal (4.9°) than the Concurrent feedback condition (2.2°). Participants in both visual feedback conditions were accurate as early as the second block, and they did not differ from each other ($p = .180$). However, a slight overcompensation occurred in the Terminal condition from the fourth to the sixth trial blocks (M = -0.35°, -0.27° and -0.41°, for blocks 4 to 6, respectively), but this effect was less evident for the Concurrent vision condition (0.16°, -0.12° and -0.08°, respectively for the fourth to the sixth trial blocks, respectively). As a result, participants in the Terminal condition aimed significantly more to the left of the target than participants in the Concurrent condition in the fourth ($p = .008$) and sixth ($p = .002$) blocks of the exposure phase. Participants in both visual feedback conditions

13

had negligible direction constant errors in the remaining trial blocks ($\underline{M}$ = 0.08° SD = .72), and they did not differ significantly from each other (p > .371). More importantly, ANOVA did not reveal a significant main effect or interaction that involved the Context factor (all p values > .163).

(Table 2 about here)

The computed ANOVA for the direction variable error (Table 2) revealed that movements performed in the Concurrent feedback condition were significantly less variable than the Terminal feedback condition, F(1, 36) = 36.48, p < .001. ANOVA also revealed a significant Visual feedback x Block interaction, F(9, 324) = 2.941, p = .013. The breakdown of this interaction into simple main effects revealed that direction variability decreased from the first to the sixth trial blocks in both the Concurrent (from 2.4° to 0.6°) and the Terminal (from 4.5° to 1.4°) conditions, F(9, 324) = 40.27, p < .001; the larger decrease in variability for the terminal condition, F(1, 36) = 36.58, p < .001, caused the interaction. No significant main effect or interactions involving the Context factor were observed (all p values > .330).

Movement trajectory (Figure 3, Table 3)

(Table 3 about here)

The small direction constant and variable errors observed at movement endpoints indicate that participants successfully adapted to the perturbation. The next analysis was performed to determine how the participants adapted their movements for the perturbation. If a side-pointing strategy was used, we should observe early movement trajectories that were directed towards the "true" target (i.e., at or around the straight ahead target) rather than towards the perturbed target (i.e., 11.4° to the right). In contrast, if early movement trajectories were directed toward the perturbed target and corrected toward the "true" target as movement unfolded, this would suggest a correction based on feedforward- and/or feedback-based control processes.

14

We computed the mean stylus position in degrees at every 10% of the total movement time for the first and for the last block of the exposure phase for each participant to determine which strategy was used during the exposure phase to counteract the prism-induced bias. The results were submitted to an ANOVA to contrast the 2 Contexts x 2 Visual feedback conditions x 2 Blocks (first vs. last) x 10 Markers (effector position at 10%, 20%, … 100% of total movement time) using repeated measurements on the last two factors.

ANOVA revealed a significant Block x Markers interaction, $F(9, 324) = 8.42$, $p < .001$. Figure 3 illustrates that the initial movement trajectory in all four groups was directed in the general direction of the 'perturbed' target rather than towards the 'true' target; this relationship was true for the first and last trial blocks. Participants aimed 7 degrees to the right of the true target up to 20% of the relative movement time. However, the mean movement trajectory was significantly redirected towards the 'true' target from this moment forward. The interaction revealed that that the movement trajectory was better aligned with the 'true' target from 40% to 100% (movement endpoint) of the relative movement time in the last block of the exposure phase rather than the first block. Notably, no significant main effect or interactions that involved either the Context factor or the Visual feedback condition was observed (all p values > 0.087).

Recalibration – realignment aftereffects comparison (Figure 4)

The recalibration test measures the proportion of the aftereffect that likely reflects the recalibration adaptive process. Three targets were presented to participants, the adaptation target and two test targets. Test targets were not presented to participants during prism exposure. Therefore, these targets provide a measure of the generalisation of the recalibration process. The exposure target should produce larger aftereffects than the two test targets because the recalibration process is thought to be specific to the exposure condition (Redding & Wallace, 2006). Finally, the realignment tests measure the proportion of aftereffects that likely reflect the realignment adaptive process. We should not observe a significant

15

aftereffect in the Virtual context according to the object unity assumption (Bedford, 1993; Redding & Wallace, 2006) because the conditions required by this assumption are not met.

We computed the aftereffects (i.e., the difference between the average movement endpoint positions in the post-test and pre-test) in the recalibration and realignment tests to test these predictions. The data were submitted to an ANOVA to contrast the 2 Tests (recalibration vs. realignment) x 2 Contexts (Natural vs. Virtual) x 2 Visual feedback conditions (Concurrent vs. Terminal) x 3 Targets (-5°, 0°, +5°) using repeated measurements on the last factor.

The left panel of Figure 4 depicts the results of the recalibration test, and the right panel illustrates the results of the realignment test. The presence of concurrent or terminal feedback did not significantly alter the aftereffect, $F(1, 36) = 0.677$, $p = 0.42$. In contrast with our expected results, the ANOVA did not reveal any significant main effect or interactions involving the target factor (all p values > .212), which indicated that the aftereffects were not significantly larger for the exposed target than the test targets. Additionally, contrary to our expectations, the ANOVA did not reveal a significant main effect of Test or any significant interaction with this factor (all p values > .242). Therefore, the aftereffects did not differ significantly from one another in the recalibration and realignment tests. Notably, ANOVA revealed a significant main effect of Context, $F(1, 35) = 30.67$, $p < .001$, which indicated that recalibration and realignment aftereffects were significantly larger in the Natural context than the Virtual context.

Discussion

The present study tested the hypothesis that prism adaptation for goal-directed movements that are performed in a virtual context results from a recalibration process rather than a realignment process because movements performed in a virtual context do not respect the requirements of the 'object unity assumption'. Larger aftereffects were expected for the trained conditions (target and initial arm configuration) and poor generalisation of these aftereffects to untrained targets and initial arm configuration because these factors are considered manifestations of the recalibration process (Clower &

16

Boussaoud, 2000). In contrast to our hypothesis, the results suggest that a realignment process occurred in our prism adaptation task regardless of a virtual or natural context. However, the magnitude of realignment was strongly dependent on the context in which the task was practiced.

A realignment process is responsible for prism adaptation in natural and virtual contexts

Contrary to our expected results, we found significant aftereffects in natural and virtual contexts conditions. In addition, no significant differences were noted between the trained and untrained initial arm configurations (recalibration test vs. realignment test) and between the exposure and the test targets (see Figure 3). Therefore, prism adaptation occurred, and it was generalisable to unexposed workspaces (Krakauer, Pine, Ghilardi, & Ghez, 2000). Additionally, the results of a supplementary analysis revealed that these aftereffects were robust because they remained significant for the last trial of the post-tests[†]. These observations are consistent with a realignment adaptive process (Clower & Boussaoud, 2000; Redding & Wallace, 2006). Therefore, the results of the current study suggest that the same process, realignment, allowed adaptation in both virtual and the natural contexts, which supports the conclusion of Norris et al. (2001).

Consistent with previous studies (Clower & Boussaoud, 2000; Norris et al., 2001), larger aftereffects were reported for all targets and the two arm configurations in the natural than the virtual context. One common characteristic between our work and the cited studies is that a 'natural condition' in which visual and proprioceptive information arose directly from the participant's hand (or very close from the hand as in Clower and Boussaoud, 2000) was contrasted with experimental conditions in which a more or less realistic representation of the participant's hand was presented on a computer/video screen. For example, participants in Norris et al.'s (2001) prismatic adaptation study performed manual aiming movements in three different contexts, i.e., natural (the hand was seen directly), video (the hand was filmed and shown in real time on a vertical computer screen) and virtual (a cursor represented the position of the hand on a vertical computer screen). They showed that the more realistic context produced larger

17

aftereffects and a better transfer of adaptation than the less realistic contexts. Taken together, these results suggest that the level of adaptation is proportional to the degree of realism of the effector representation.

Adaptation depends on the degree of congruency between visual and proprioceptive/motor feedback of the effector

The data of Norris et al. (2001) clearly show that the aftereffects following prism adaptation are largely dependent on the level of congruency between visual and proprioceptive/motor feedback relative to the hand/effector position. Norris and colleagues suggested that the aftereffects were larger in the natural task because participants relied heavily on visual feedback for movement planning and control, and they progressively increased their reliance on proprioceptive feedback as the task became more abstract. However, we recently produced evidence indicating that reliance on visual feedback increased rather than decreased as the visual context became less realistic (Veilleux & Proteau, 2011b). Therefore, it is unlikely that the larger aftereffects observed in natural contexts compared to virtual contexts result from an increased reliance on visual information. Rather, we suggest that the larger aftereffects that were observed for the more natural condition compare to the less natural conditions reflect the degree to which proprioceptive and visual feedback are realigned with one another. This realignment process depends on the degree of spatial and/or morphological congruency that exists between these two sources of feedback. For example, increasing the congruency between visual and proprioceptive feedback in virtual contexts could be performed by presenting the following conditions: (a) the effector's visual information on an aligned display (vs. a non-aligned display; see Veilleux and Proteau, 2011b); (b) real time video representation of the hand (vs. a cursor) or (c) a three dimensional representations of the hand (vs. two dimensions).

The capacity of the brain to modulate the extent to which vision and proprioception are bound together is not unique to prism adaptation, and it is well apparent in the 'rubber hand illusion'. In the latter case, the participant's hand is hidden, but a realistic rubber hand is visibly aligned with it (Armel &

18

Ramachandran, 2003; Botvinick & Cohen, 1998). If the real hand and rubber hand are being stroke with a paintbrush synchronously, the participant will feel the rubber hand as their own (Costantini & Haggard, 2007; IJsselsteijn, De Kort, & Haans, 2006). Following this synchronous stroking of the real and rubber hands, participants were asked to use their right index finger to point towards the index finger of the left hand (the hand side experiencing the illusion) with their eyes closed. Participants' reaches were displaced toward the rubber hand. This illusion indicates that there is a drift of the proprioceptive map towards the visual map that encodes the location of the rubber hand (Botvinick & Cohen, 1998; Rohde, Di Luca, & Ernst, 2011). Therefore, the rubber hand illusion creates a situation in which visual and proprioceptive representations of the divergent hand are realigned in a convergent multisensory map, which is similar to prism adaptation.

As in the present study, the rubber hand illusion is modulated by the visual and proprioceptive congruency of the participant's hand and the rubber hand. The following factors specifically reduced or eliminated the illusion: (a) a spatial misalignment of the rubber hand and real hand (Armel & Ramachandran, 2003), (b) asynchronous brushing of the rubber hand and real hand (Armel & Ramachandran, 2003), and (c) presentation of the rubber hand and brushing action using a video rather than a live presentation (IJsselsteijn et al., 2006). In addition, the strength of the illusion increased activation of a region of the ventral premotor cortex (Ehrsson, Spence, & Passingham, 2004) that is thought to represent the seen and felt position of the hand (Graziano, 1999; Graziano, Cooke, & Taylor, 2000; Graziano, Hu, & Gross, 1997; Graziano, Yap, & Gross, 1994). Taken together, the results of the present study and the results reviewed above suggest that if the seen and felt positions of the effector are perceived as belonging to oneself, i.e., the feeling of ownership, and if there is a mismatch between these two sensory representations of this effector, then a strong and in depth realignment process is activated.

Recalibration processes during the exposure phase is achieved through distinct strategies

19

In contrast with the aftereffects data, the exposure data did not show evidence that the processes that lead to the elimination of the perturbation differed across conditions. Therefore, this result does not support our hypothesis that the availability of visual feedback during movement execution influences the detection of a misalignment. Rather, it was shown that participants in all four experimental groups chose between two different strategies to eliminate the prism-induced bias. The most popular strategy consisted of reducing, but not eliminating, the initial direction bias through an offline modification of the movement plan (see average and typical trials A in Figure 5). The initial movement trajectory remained directed towards the 'perturbed' target, and participants implemented a change in movement direction at approximately half-way through the movement (O'Shea et al., 2014). This movement reversal brought the effector close to or in the vicinity of the 'true target'. Whether this change in movement direction was based on feedforward and/or on feedback processing is unknown presently. However, the fact that this behaviour was observed in the concurrent and terminal visual feedback conditions suggests a feedforward or proprioceptive feedback loop (Desmurget & Grafton, 2000; Veilleux & Proteau, 2011a). Some participants showed a distinct pattern to eliminate the perturbation (see typical trials B in Figure 5). Quickly after introducing the prism perturbation, some participants chose to aim directly at the 'true' target or in a direction opposite to the perturbation. This behaviour has been called a 'side-pointing' strategy (Newport & Jackson, 2006; Redding & Wallace, 2006), and it suggests that participants compensated for the perturbation only through a modification of the movement plan. The current set of data suggest that the selection of one strategy over the other one was not influenced by the type of visual feedback (concurrent vs. terminal) or the context in which the task was performed.

Conclusions

Our results indicate that virtual and natural contexts trigger the same realignment process to achieve adaptation in response to prism perturbation. However, the degree to which one will adapt is a function of the congruency between vision and proprioception/motor feedback.

20

Acknowledgments

21

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23

Figure Captions

Figure 1. Illustration of the experimental setup.

Figure 2. Direction constant (upper panel) and variable error (lower panel) in degrees as a function of practice, contexts and visual feedback conditions.

Figure 3. Position of the effector (in degrees) at every 10% of movement time trajectory. Left panel: first block of trials during the exposure phase; Right panel: last block of trials during the exposure phase.

Figure 4. Aftereffects of the recalibration test (left panel) and realignment test (right panel) as a function of targets, contexts and visual feedback conditions.

Figure 5. Position of the effector (in mm) at every 5% of movement trajectory as a function of Contexts and Visual Feedback conditions. Left panel: averaged movement trajectories. Middle panel: Typical trial (A) of one participant representing a mixed offline/online strategy for error reduction. Right panel: Typical trial (B) of one participant representing an offline strategy for error reduction.

24

Footnote

Table 1. Mean (SD) Directional Constant Error (°) as a Function of the Experimental Contexts, the Visual Feedback and the Blocks of Trials

Context	Visual feedback	Blocks									
		1	2	3	4	5	6	7	8	9	10
Virtual	Terminal	1.98	-0.13	-0.21	-0.13	-0.19	-0.24	-0.11	-0.16	-0.19	-0.20
		(1.39)	(0.42)	(0.41)	(0.30)	(0.43)	(0.37)	(0.32)	(0.43)	(0.32)	(0.47)
	Concurrent	5.77	0.34	-0.20	-0.24	-0.20	-0.31	-0.05	0.19	-0.13	-0.03
		(2.27)	(1.11)	(1.33)	(0.67)	(0.79)	(0.60)	(0.74)	(0.54)	(0.66)	(1.03)
	Terminal	2.33	0.05	0.26	0.44	-0.05	0.07	0.70	0.23	0.05	0.13
		(1.29)	(0.57)	(0.75)	(0.41)	(0.46)	(0.45)	(1.05)	(0.37)	(0.29)	(0.25)

	)	)	)	)	)	)	)	)	)	)
Natural										
Concurrent	4.05	0.36	0.44	-0.47	-0.33	-0.51	0.26	0.19	0.30	0.03
	(2.81	(1.11	(0.88	(0.97	(0.56	(0.33	(1.32	(0.61	(0.77	(0.60
	)	)	)	)	)	)	)	)	)	)

27

Table 2. Mean (SD) Variable Error (°) as a Function of the Experimental Contexts, the Visual

Feedback and the Blocks of Trials

Context	Visual feedback	Blocks									
		1	2	3	4	5	6	7	8	9	10
Virtual	Terminal	2.49	0.55	0.66	0.67	0.62	0.61	0.77	0.59	0.60	0.63
		(1.28)	(0.33)	(0.25)	(0.42)	(0.21)	(0.17)	(0.18)	(0.18)	(0.34)	(0.25)
	Concurrent	4.76	1.69	1.71	1.56	1.53	1.56	1.24	1.71	0.91	1.02
		(1.65)	(0.74)	(0.99)	(0.72)	(0.37)	(0.51)	(0.74)	(0.95)	(0.42)	(0.51)
	Terminal	2.25	0.71	0.87	0.64	0.82	0.63	1.32	0.58	0.61	0.59

Natural	(1.54)	(0.48)	(0.56)	(0.25)	(0.65)	(0.25)	(1.68)	(0.25)	(0.25)	(0.35)
Concurrent	4.17	1.17	1.75	1.51	1.20	1.62	1.52	1.80	1.60	1.75
	(2.37)	(0.65)	(1.18)	(0.71)	(0.51)	(0.69)	(0.70)	(0.76)	(1.13)	(0.67)

29

Table 3. Mean (SD) of the Effector Position in Degrees (°) as a Function of the Experimental Contexts, the Visual Feedback Conditions, the Blocks of Trials and Percent of Movement Time Trajectory

Context	Visual Feedback	Blocks	Percent of Movement Trajectory (%)									
			10	20	30	40	50	60	70	80	90	100
Virtual	Terminal	First	8.6	7.4	6.2	5.2	4.2	3.3	2.8	2.5	2.4	2.2
			(9.2)	(6.7)	(5.3)	(4.2)	(3.4)	(2.7)	(2.1)	(1.7)	(1.7)	(1.7)
		Last	8.8	6.4	4.7	3.3	2.3	1.4	0.8	0.5	0.4	0.3
			(11.6)	(8.6)	(6.7)	(5.1)	(3.8)	(2.8)	(1.8)	(1.1)	(0.7)	(0.6)
	Concurrent	First	7.4	6.1	5.1	4.2	3.4	2.6	1.9	1.6	1.3	1.2
			(5.0)	(3.3)	(2.9)	(2.5)	(1.9)	(1.3)	(0.9)	(0.7)	(0.7)	(0.8)
		Last	6.5	4.9	3.8	2.8	1.9	1.1	0.5	0.2	0.1	0.1
			(5.8)	(4.0)	(3.2)	(2.6)	(1.8)	(1.0)	(0.5)	(0.3)	(0.2)	(0.2)

	First	9.4	8.2	7.4	6.3	5.1	4.2	3.6	3.2	3.1	3.1
		(5.1)	(3.2)	(3.0)	(2.7)	(2.2)	(1.7)	(1.3)	(1.4)	(1.6)	(1.6)
Terminal											
	Last	11.1	9.2	7.5	5.8	4.1	2.5	1.3	0.4	-0.1	-0.2
		(8.1)	(5.6)	(4.6)	(3.9)	(3.2)	(2.4)	(1.7)	(1.1)	(0.8)	(0.7)
Natural											
	First	7.9	7.1	6.3	5.3	4.1	3.0	2.1	1.5	1.1	1.0
		(7.9)	(5.5)	(4.5)	(3.6)	(2.7)	(1.9)	(1.3)	(1.0)	(0.8)	(0.8)
Concurrent											
	Last	9.6	7.7	5.9	4.4	2.9	1.7	0.8	0.2	-0.1	-0.1
		(6.1)	(4.4)	(3.6)	(2.9)	(2.0)	(1.3)	(0.8)	(0.5)	(0.4)	(0.4)

31

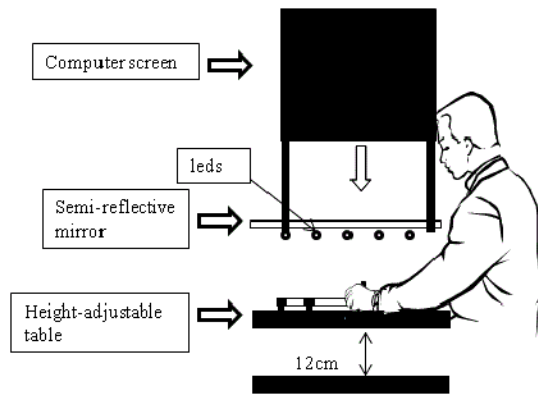Computer screen

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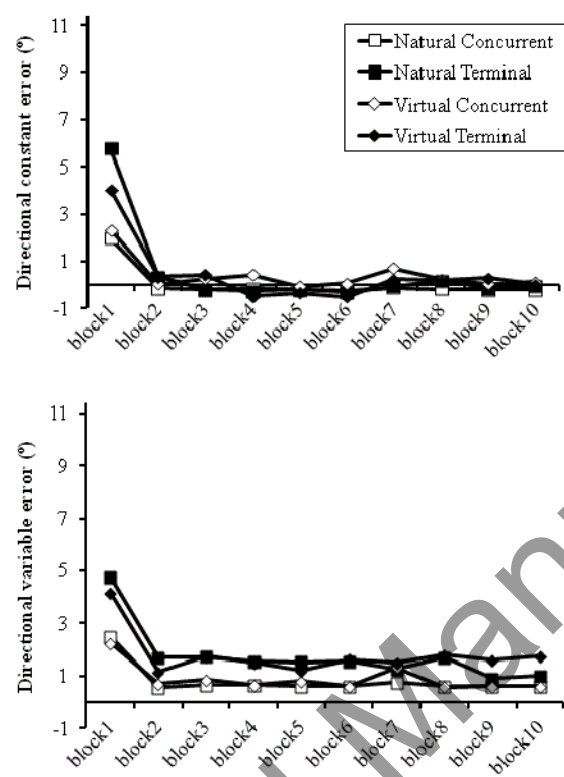
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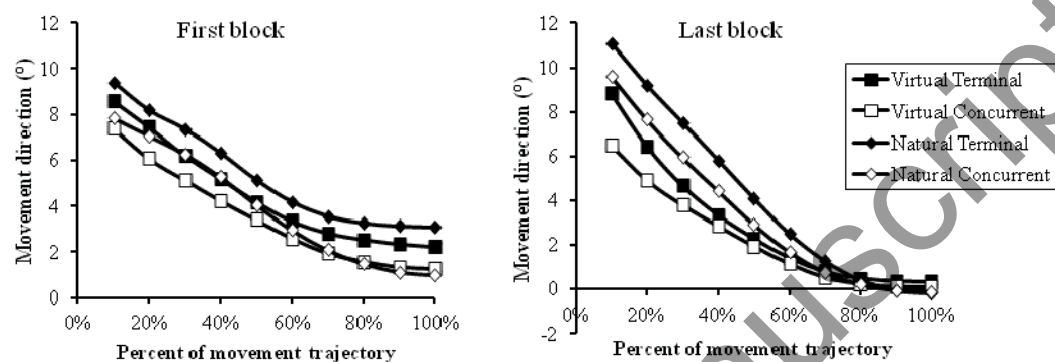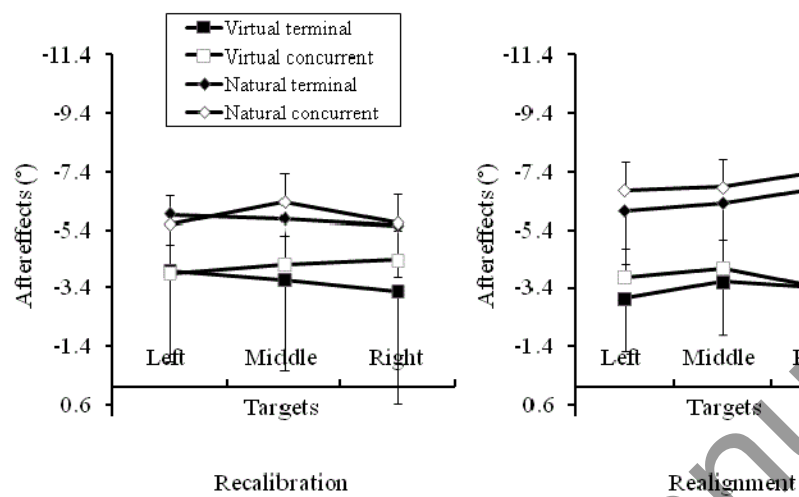
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Figure 1.

Figure 2.
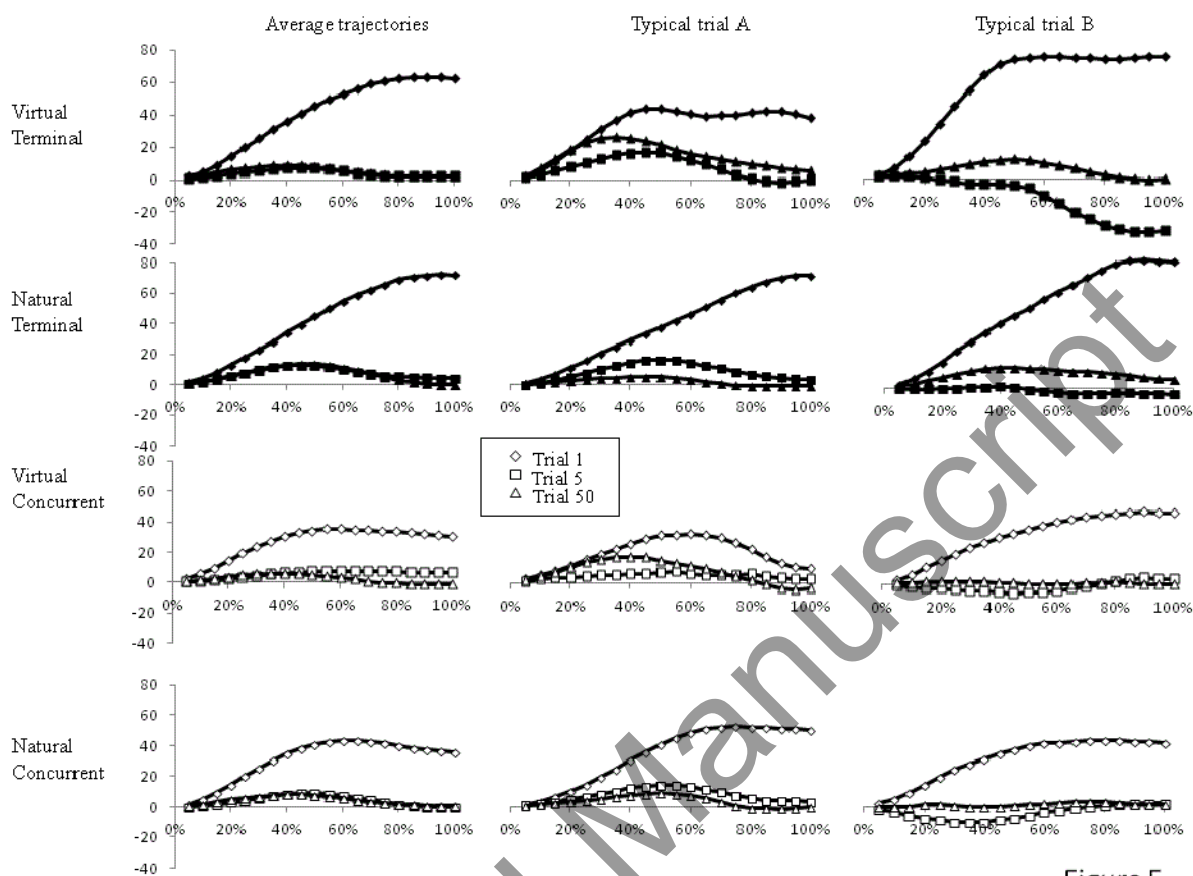
Figure 3.

34

Figure 4.

Figure 5.

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† We calculated a supplementary analysis to determine whether the aftereffects remained significant at the end of the post-test. Specifically, we computed an ANOVA that contrasted 2 Contexts x 2 Visual feedback conditions x 2 Tests (recalibration vs. realignment) x 3 Targets x 2 Trials (Average of pre-test vs. 10th trial of post-test) using repeated measures on the last three factors. The ANOVA revealed a significant Context x Trials interaction, $F(1, 36) = 10.50$, $p = .003$, which indicated that the position of the effector at movement endpoint at the end of the post-tests was located significantly more to the left than during the pre-test $6.3° \pm 3.3°$ on the first trial to $4.7° \pm 3.2°$ on the last trial. In light of these results, it was assumed that there was no significant decrease in aftereffects even after 60 post-adaptation trials.

36