

Direction of Visual Shift and Hand Congruency Enhance Spatial Realignment During Visuomotor Adaptation

Christopher L. Striemer, Adam Morrill

The final publication is available at Springer via

<http://dx.doi.org/10.1007/s00221-023-06697-4>

Permanent link to this version <https://hdl.handle.net/20.500.14078/3483>

License All Rights Reserved

**Direction of visual shift and hand congruency
enhance spatial realignment during visuomotor adaptation.**

Christopher L. Striemer ^{1,2*} & Adam Morrill ¹

1. Department of Psychology, MacEwan University, Edmonton, Alberta, Canada

2. Neuroscience and Mental Health Institute, University of Alberta, Edmonton, Alberta, Canada

* Corresponding Author
Christopher L. Striemer, PhD
Associate Professor
Department of Psychology
MacEwan University
10700 – 104 Avenue
Edmonton, Alberta, Canada, T5J 4S2
Email: striemerc@macewan.ca
Phone: 780-633-3467

Abstract

Although prism adaptation has been studied extensively for over 100 years to better understand how the motor system adapts to sensory perturbations, very few studies have systematically studied how the combination of the hand used to adapt, and the direction of visual shift, might influence adaptation. Given that sensory inputs and motor outputs from the same side are processed (at least initially) in the same hemisphere, we wondered whether there might be differences in how people adapt when the hand used and the direction of visual shift were congruent (e.g., adapting to rightward shifting prisms with the right hand), compared to incongruent (e.g., adapting to rightward shifting prisms with the left hand). In Experiment 1 we re-analyzed a previously published dataset (Striemer, Enns, & Whitwell, 2019) in which healthy adults ($n=17$) adapted to 17° leftward or rightward optically displacing prisms using their left or right hand (tested in separate sessions, counterbalanced). Our results revealed a “congruency effect” such that adaptation aftereffects were significantly larger for reaches performed without visual feedback (i.e., straight-ahead pointing) when the direction of prism shift and the hand used were congruent, compared to incongruent. We replicated this same congruency effect in Experiment 2 in a new group of participants ($n=25$). We suggest that a better understanding of the cognitive and neural mechanisms underlying the congruency effect will allow researchers to build more precise models of visuomotor learning, and may lead to the development of more effective applications of prism adaptation for the treatment of attentional disorders following brain damage.

Keywords: prism adaptation, visuomotor adaptation, motor learning, cerebellum, posterior parietal cortex

Introduction

Although the ability to adjust our movements based on errors seems simple, it involves complex interactions between cortical and sub-cortical brain regions (e.g., Clower et al., 1996; Danckert, Ferber, & Goodale, 2008; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Welch & Goldstein, 1972). One paradigm that has been widely used to study visuomotor learning is prism adaptation (PA)(Redding, Rossetti, & Wallace, 2005). During PA, the participant is asked to wear a pair of glasses that shifts their vision in one direction, for example 15° to the right, while reaching to targets. Initially, the participant's reaches will miss in the direction of the prism shift (e.g., to the right). The internally generated "error signal" that is created when the participant's reach misses to the right of the target is used to adjust future reaches *leftward* to compensate. Previous research suggests that the "strategic recalibration" that occurs during the first few reaches relies on the posterior parietal cortex (PPC)(Chapman et al., 2010; Clower et al., 1996; Danckert et al., 2008; Luaute et al., 2009; Mutha, Sainburg, & Haaland, 2011; Pisella et al., 2004; Pisella, Rode, Farné, Tilikete, & Rossetti, 2006).

If the participant continues to reach with prisms on (e.g., 50+ reaches) then "spatial realignment" occurs where the spatial reference frames for the eye and the hand realign to adjust for the error induced by the visual shift (Redding et al., 2005; Redding & Wallace, 2006). This is indexed by aftereffects that occur in the direction *opposite* the prism shift. For example, following rightward PA, if the participant is asked to close their eyes and point straight-ahead (referred to as straight-ahead pointing), they typically point to the left of true midline because of the leftward spatial realignment that occurred in response to the rightward prism shift (Redding et al., 2005). Previous research suggests that spatial realignment relies on the cerebellum (e.g., Baizer, Kralj-Hans, & Glickstein, 1999; Bossom, 1965; Martin et al., 1996; Norris, Hathaway,

Taylor, & Thach, 2011; Pisella et al., 2005; Weiner, Hallett, & Funkenstein, 1983; Welch & Goldstein, 1972; Werner, Bock, Gizewski, Schoch, & Timmann, 2010).

During a movement sensory inputs and motor outputs on the same side are processed (at least initially) in the same hemisphere in both the cerebral cortex (i.e., the contralateral hemisphere), and the cerebellum (i.e., the ipsilateral hemisphere) (Kolb & Whishaw, 2009; Nolte, 2002). Given this, we wondered whether PA would be differentially influenced by the combination of the hand used to adapt, and the direction of visual shift. Specifically, we wondered whether PA and its aftereffects would differ under conditions where the hand used and the direction of visual shift were congruent (e.g., adapting to right prisms with the right hand) and visual inputs and motor outputs were initially processed in the same hemisphere, compared to incongruent (e.g., adapting to right prisms with the left hand), in which the visual inputs and motor outputs would initially be processed in opposite hemispheres. If PA differs depending on the congruency of the visual shift and the hand used to adapt, it could have important implications for models of PA, and visuomotor learning more generally.

Interestingly, although PA has been studied for well over 100 years (Von Helmholtz, 1867), to our knowledge, very few studies have systematically examined how prism adaptation aftereffects might be influenced by a combination of both the hand used during adaptation (left vs. right), and the direction of visual shift (left vs. right). Instead, most studies involving prism adaptation have only examined one direction of visual shift with the dominant (i.e., right) hand (e.g., Martin et al., 1996), compared different groups of people adapting to different directions of prism shift with the same hand (e.g., Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; C. Michel et al., 2003; Rossetti et al., 1998), alternated the direction of prism shift in the same individuals, but only used the dominant hand to adapt (e.g., Clower et al., 1996), or alternated the hand used

to adapt, but only used one direction of prism shift (e.g., Carine Michel, Vernet, Courtine, Ballay, & Pozzo, 2008; Reed & Dassonville, 2014).

To directly examine the relationship between how the direction of visual shift and the hand used to adapt might influence PA, in Experiment 1 we re-analyzed healthy control data (n=17) from a previously published dataset in which we demonstrated that a patient who was completely blind to static stimuli was still able to adapt to left or right prisms with the left or the right hand (Striemer, Enns, et al., 2019). This new analysis revealed a “congruency effect” such that the healthy control participants demonstrated a larger shift in straight-ahead pointing (a measure of proprioceptive shift) when the direction of visual shift and the hand used to adapt were “congruent” (e.g., right hand, right prisms), compared to incongruent (e.g., left hand, right prisms). In Experiment 2 we replicated the same effect in a different group of healthy adults (n=25). In combination, these results suggest that prism adaptation is enhanced when the visual inputs and motor outputs used during adaptation are processed in the same cerebral or cerebellar hemisphere, compared to opposite hemispheres.

Experiment 1.

Methods

Experiment 1.

Note that all data from Experiment 1 are a re-analysis of previously published control participant data from Striemer and colleagues (Striemer, Enns, et al., 2019).

Participants.

As noted in our previous manuscript (Striemer, Enns, et al., 2019), the healthy control participants consisted of 17 right-handed adults (mean age = 24 years; SD = 6.4; 9 males; all right-handed). Testing occurred at MacEwan University in Edmonton, Alberta, Canada. Participants provided written informed consent and were compensated with either course credit, or \$10 per hour of participation. All experimental procedures were approved by the MacEwan University Research Ethics Board.

Study design.

The study was conducted as a within-subject design such that each participant adapted to both leftward and rightward shifting prisms with the left or the right hand. Each participant attended two different 1-hour long testing sessions separated by at least 24 hours. The hand used to adapt to prisms was manipulated between testing sessions (e.g., left hand in session 1 and right hand in session 2), whereas the direction of prism shift was manipulated within a session (e.g., left prisms followed by right prisms). The order in which each hand (between sessions) and each direction of prism shift (within sessions) was tested first, was counterbalanced across participants.

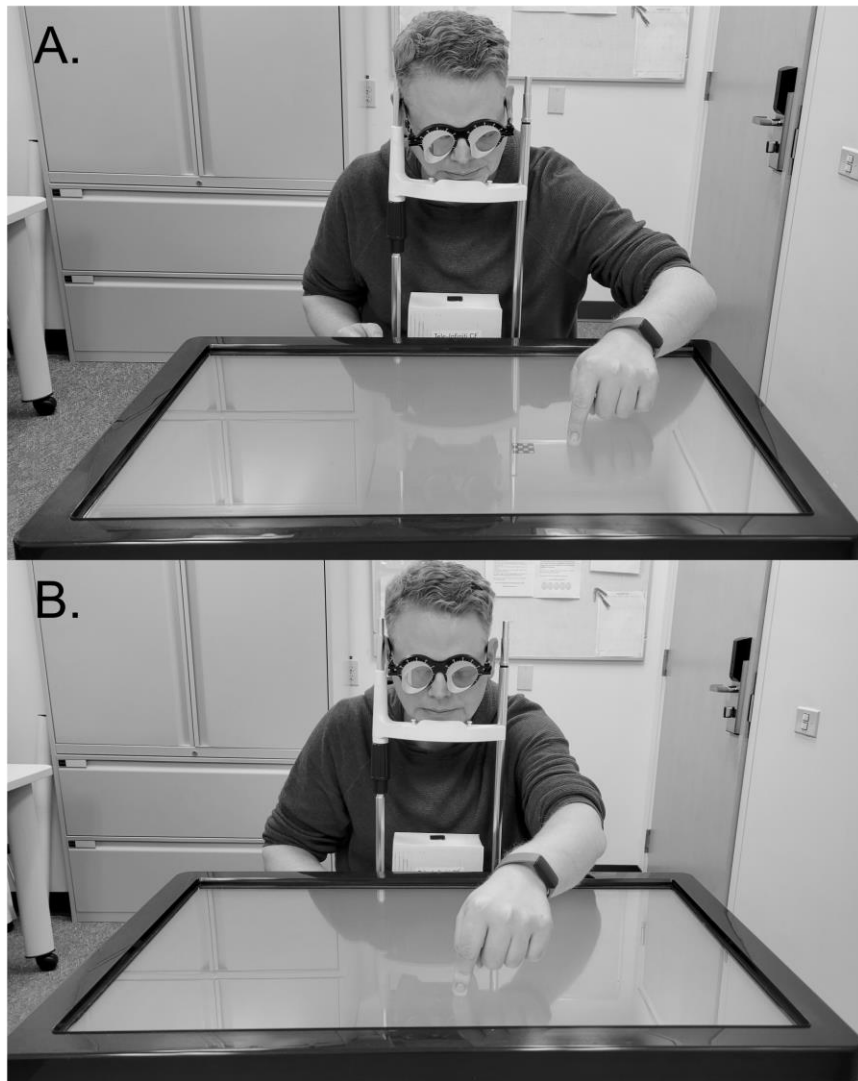
Experimental setup and procedure.

Participants were seated at a table with their head in chin rest 45 cm away from a 32'' wide screen touch screen (ELO touch systems, 60 Hz refresh, 1366 x 768 resolution; Figure 1). The touchscreen was mounted horizontally and was used to record touch endpoints. Participants sat with their hand resting on a small platform, which served as the “home” position directly in front of the chinrest. This ensured that movements from the home position to the touchscreen were

performed with a comfortable and slightly downward trajectory. For each pointing trial, participants would begin with their index finger (of the left or right hand, depending on the testing session) in the “home” position. This same basic setup was used in two different pointing tasks: 1) a target directed pointing task (TDP) in which participants pointed to visible targets before, during, and after PA, and 2) a straight-ahead pointing (SAP) task in which participants were asked to point straight ahead from their body midline with their eyes closed (i.e., without visual feedback). Both pointing tasks are described in detail below.

--Insert Figure 1 here--

Figure 1. Depicts the experimental setup for testing control participants in Striemer and colleagues (2019), as well as the replication study carried out in Experiment 2. See Methods section for details. A) depicts a trial in the target directed pointing (TDP) task in which participants were asked to reach to a square checkerboard (or circle in Experiment 2) target as quickly and accurately as possible with prisms off (during baseline and “washout” TDP), or prisms on (during the adaptation phase). In this example the participant is reaching to a left target with the left arm while wearing leftward shifting prisms. B) Depicts a single trial of the straight-ahead pointing (SAP) task in which the participant is asked to close their eyes and point straight ahead of their body midline.



Target directed pointing (TDP).

The basic setup of the TDP task was as described above. At the beginning of each trial in the TDP task the experimenter pressed a key which initiated a randomly selected delay of either 500, 750, 1000 or 1250 msec. After this randomized delay, a single target appeared on the touchscreen 10° to the left or right of midline and 35 cm from the “home” position. The target stimulus was a square 2 x 2cm black and white checkerboard that rapidly alternated in contrast every 125 msec, for 1 second (i.e., 4Hz). A flickering checkerboard was used as the target because the current dataset originally served as a control group for a previously published study with patient MC (Striemer, Enns, et al., 2019), who is completely blind to static stimuli following bilateral lesions to the occipital lobes and ventral-temporal cortex. However, MC’s motion sensitive regions V5/MT were undamaged, and she thus retained the ability to detect motion, without being able to identify the moving object (Arcaro et al., 2018). This flickering target was sufficient to engage MC’s intact motion detection system (Striemer, Whitwell, & Goodale, 2019) and allowed her to aim her reach towards a target which was necessary to adapt her prisms. After the target flickered at 4Hz for 1 second, a still image of the checkerboard remained on the touchscreen and a 1000 Hz tone was played. The participant was instructed to not initiate a reaching movement until they heard the tone. The last frame of the checkerboard remained visible until the participant touched the screen. Participants were told to reach out to touch the target as swiftly and as accurately as they could, using their index-finger, and the first touchpoint registered by the screen was recorded. Following contact with the screen, the target disappeared, and the participant returned their finger to the “home” position to await the next trial. For all TDP trials, the initial position of the hand was obstructed by the chin rest, but vision

of the hand and the target were visible during the reach (i.e., concurrent feedback). Each block of TDP contained an equal number of left and right targets that were presented in a random order.

Straight-ahead pointing (SAP).

SAP was used to measure PA aftereffects. During the SAP task participants were asked to close their eyes and point straight-ahead from their body midline and then touch the surface of the touch screen where the endpoint was recorded. This open loop pointing task is commonly used to measure proprioceptive shift that has occurred in response to PA (Redding et al., 2005). Each block of the SAP task contained 5 trials. One block of SAP was run prior to the baseline TDP task (i.e., baseline SAP), another block of SAP was run after 100 trials of TDP with prisms on (i.e., “halfway SAP”), and the final block of SAP was run immediately after the TDP with prisms on (i.e., “post-prisms SAP”), but prior to washout TDP (see below for details). The SAP task was always completed with the same hand that was used to adapt to prisms.

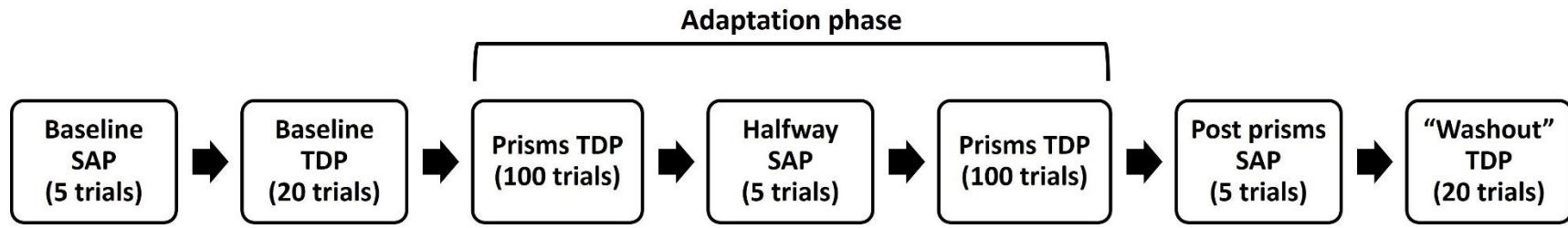
Prism adaptation (PA) procedure.

Prior to PA the participant completed 20 trials of TDP task to measure baseline pointing. In a single run of PA, 200 trials of the TDP task were completed with the left or the right hand while wearing 17° (30 diopter) leftward or rightward shifting prisms (Bernell, USA). Each run of 200 trials was comprised of two blocks of 100 trials separated by a short break, and one block of the SAP task (halfway SAP). Following PA, one more block of SAP was completed, followed by 20 more trials of the TDP which we refer to as the “washout” phase as the participant is de-adapting from the prisms. Note that during the first few trials of washout phase post prisms, if the participant successfully adapted, then they should miss the target in the direction opposite the

prism shift. Given that both the target and the hand were visible during washout phase, the first few trials of washout pointing are thought to measure both visual and proprioceptive shift induced by PA (Redding et al., 2005). The order of events in a single PA run (i.e., one hand, one direction of prism shift) is depicted in Figure 2. Note that two separate runs of PA were completed within a single 1-hour testing session with the same hand used, but changing the direction of prism shift between adaptation runs (see Study Design above). This was done to avoid potential contamination via inter-manual transfer from the adapted to the non-adapted hand within a testing session (Redding et al., 2005; Redding & Wallace, 2009).

--Insert Figure 2 here--

Figure 2. Depicts the sequence of events for one run of prism adaptation. The same procedure was completed four times in total, once for each hand (left vs. right) by prism shift (left shift vs. right shift) combination. SAP=straight-ahead pointing. TDP=target directed pointing. See Methods for descriptions of each of these tasks.



Data analysis.

For both the TDP and SAP tasks, we measured the horizontal (i.e., 'X') pointing error on each trial as the distance between the center of the target and the recorded finger landing location on the touch screen where negative values were leftward and positive values were rightward. These data were then used to analyze various aspects of PA and its aftereffects as described below. All statistical analyses were carried out using JASP (JASP-Team, 2022).

Results

Target directed pointing (TDP) and washout pointing.

All target direct pointing data for Experiment 1 are reported in Figure 3a and Supplementary Table 1. First, we confirmed that participants were able to adapt to prisms in the expected direction for each hand (left vs. right) by prism shift (left vs. right) combination. To examine this, we compared the average pointing error for the 20 baseline (pre-prism) TDP trials with the average pointing error for the first 5 trials of TDP during the “washout” (i.e., post-prisms) phase using paired samples t-tests. This analysis confirmed that participants were able to adapt to leftward shifting prisms with the left hand (pre=-.42cm, vs. post=3.14cm; $t(16)=7.37, p<.001$) and the right hand (pre=-.12cm vs. post=2.41cm; $t(16)=5.12, p<.001$). In addition, participants were able to adapt to rightward shifting prisms with the left hand (pre=.11cm vs, post=-3.93; $t(16)=6.85, p<.001$) and the right hand (pre=.44cm vs. post=-3.04; $t(16)=6.24, p<.001$).

Next, we examined whether there were differences in the *magnitude* of the aftereffects induced by prisms for each hand by prism shift combination by taking the absolute difference in pointing error for the average of the first 5 trials of TDP during the “washout” (i.e., post-prisms) phase and the average baseline (i.e., pre-prisms) pointing error. A within-subject ANOVA with

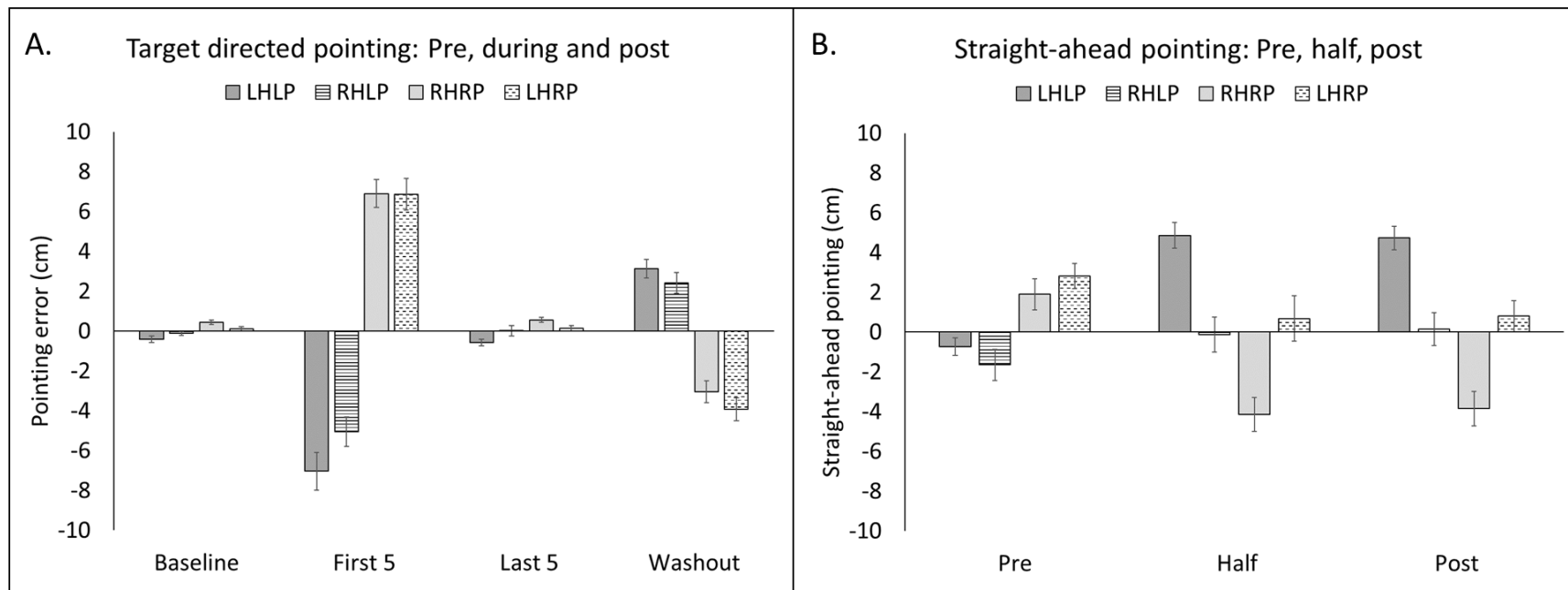
hand (left vs. right) and prism shift (left shift vs. right shift) as the within-subject factors revealed a marginal main effect of prism shift ($F(1,16)=4.26$, $p=.056$, $\eta^2_p=.21$) such that rightward shifting prisms (3.76cm) led to somewhat larger aftereffects than leftward shifting prisms (3.19cm). No other effects were significant.

We then examined the magnitude of initial pointing errors during the PA phase by calculating the absolute difference in pointing error for the average of the first five pointing trials during PA and the average of the 20 baseline trials completed prior to PA. A within-subject ANOVA with hand (left vs. right) and prism shift (left shift vs. right shift) revealed no main effects or interactions (all p 's $>.14$).

Finally, we examined pointing error reduction by calculating the absolute difference in pointing errors for the average of the first 5 trials with prisms on and the average pointing error for the last 5 trials with prisms on. A hand (left vs. right) by prism shift (left shift vs. right shift) ANOVA, once again, revealed no significant main effects or interactions (all p 's $>.20$).

--insert Figure 3 here--

Figure 3. A) Average pointing error (in cm) for the target directed pointing task at baseline, as well as for the first five trials during prism adaptation (First 5), the last five trials during prism adaptation (Last 5) and the first five trials of the Washout phase following adaptation (Washout). Note that during the first five trials during adaptation, the participant misses in the direction of the prism shift. However, by the last five trials during adaptation, the participant has significantly reduced their pointing errors. An aftereffect is demonstrated during the washout phase when the prisms are removed, and the participant now reaches in the direction opposite the prism shift. **B)** Average straight-ahead pointing (SAP) data (in cm) pre, halfway, and post adaptation. For SAP, aftereffects are demonstrated when the participant reaches in the direction opposite the prism shift halfway and/or post adaptation. For both Figures, positive values are to the right of center, negative values are to the left of center. Error bars represent the standard error. These data are a re-analysis of controls participants from Striemer and colleagues (2019).



Straight-ahead pointing (SAP).

The straight-ahead pointing data for Experiment 1 are reported in Figure 3b and Supplementary Table 2. First, we wanted to verify that participants were able to adapt in the expected direction, as measured by SAP, for each hand by prism shift combination. To examine this, we used separate one-way within-subject ANOVAs with time (pre, halfway, post) at the within-subject factor. This revealed that, for each hand by prism shift combination, there was a significant overall effect of time (all F 's >4.23 , all p 's $<.023$). In addition, for each hand by prism shift combination, Holm corrected posthoc tests (Holm, 1979) revealed that there was a significant difference in SAP in the expected direction (i.e., opposite the prism shift) between pre and halfway SAP (all t 's >2.59 , all p 's $\leq .043$, Holm corrected), as well as pre and post SAP (all t 's >2.44 , all p 's $\leq .043$, Holm corrected). However, there were no significant differences between halfway and post SAP (all p 's $>.61$). In short, participants had no trouble adapting to leftward or rightward shifting prisms with either hand as measured by SAP.

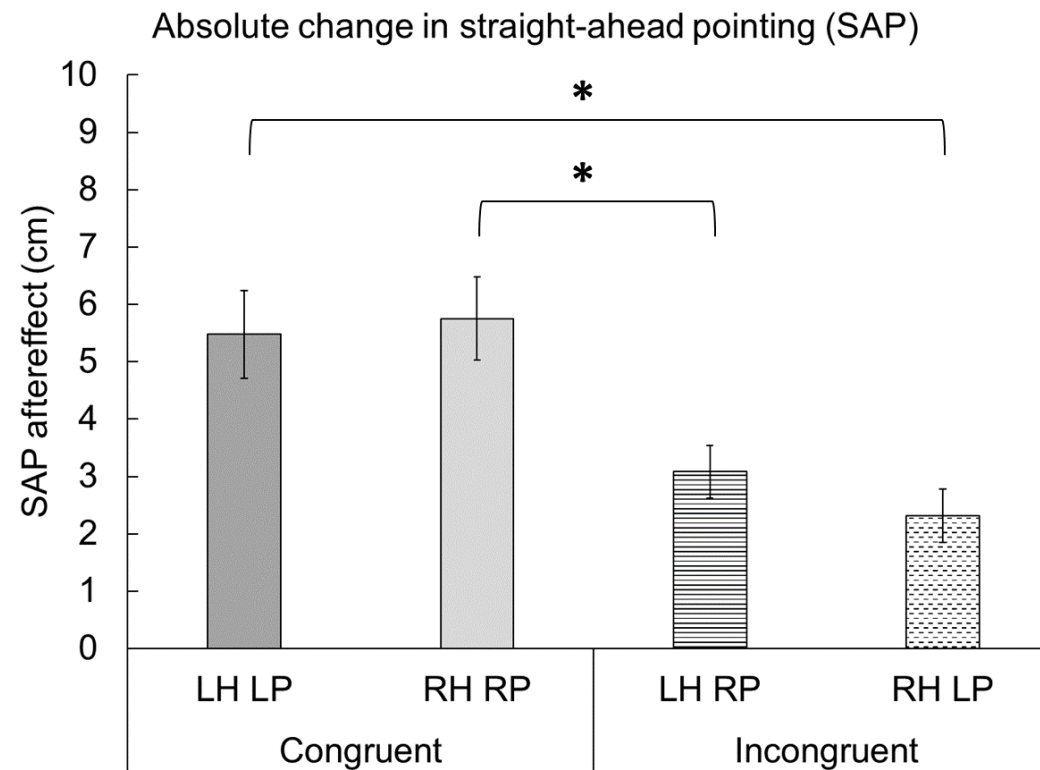
Next, we wanted to examine whether there were any differences in the *magnitude* of the aftereffects induced by prisms on SAP for each hand by prism shift combination. To determine this, we compared the absolute difference in SAP between the baseline (i.e., pre-prisms) and post-prisms SAP blocks for each hand by prism shift combination using a within-subject ANOVA with hand (left vs. right) and prism shift (left shift vs. right shift) as the within-subject factors. This analysis revealed a significant hand x prism shift interaction ($F(1,16)=15.09$, $p=.001$, $\eta^2_p=.49$). No other effects were significant.

To further examine the hand x prism shift interaction for SAP, we compared the simple main effect of hand for each direction of prism shift. This analysis indicated that there was a significant difference in the magnitude of the aftereffect induced by prisms (as measured by

SAP) between the two hands for both leftward shifting prisms (left hand=5.48cm vs. right hand=2.32cm; ($F(1)=17.68$, $p<.002$, Holm corrected), as well as rightward shifting prisms (left hand=3.09cm vs. right hand=5.75cm; ($F(1)=6.90$, $p=.018$, Holm corrected). Specifically, this analysis revealed that the aftereffect was larger when the hand and the direction of prism shift were congruent (i.e., left hand-left prisms or right hand-right prisms) compared to incongruent (i.e., right hand-left prisms or left hand right-prisms; Figure 4).

--insert Figure 4 here--

Figure 4. Depicts the absolute change in straight-ahead pointing (SAP) pre vs. post prism adaptation based on the re-analysis of control data from Striemer and colleagues (2019). Data are presented as a function of hand used (left hand=LH, right hand=RH) and direction of prism shift (leftward shifting prisms=LP, rightward shifting prisms=RP). Data are depicted in centimeters (cm). Error bars represent the standard error. * indicates $p < .05$.



Interim Discussion

To examine whether the magnitude of PA aftereffects were influenced by the hand used and the direction of prism shift, we reanalyzed control data ($n=17$) from a previously published dataset (Striemer, Enns, et al., 2019). Results from washout TDP revealed that, although participants were able to adapt to leftward or rightward shifting prisms with the left or the right hand, there were no significant differences in the magnitude of aftereffects. In addition, there were no significant differences in the magnitude of initial prism error, or pointing error reduction, between the different hand by prism shift combinations.

However, the analysis of the SAP data told a different story. Again, participants were able to adapt to leftward and rightward shifting prisms with the left or the right hand. In addition, when we analyzed the magnitude of the aftereffects generated via SAP, we observed a significant hand by prism shift interaction such that the aftereffects were larger when the hand and the direction of prism shift were congruent (i.e., left hand-left prisms or right hand-right prisms) compared to incongruent (e.g., left hand- right prisms or right hand-left prisms). These results could have important implications for our understanding of how proprioceptive and visual error signals are integrated during PA. But first, to ensure that these results were reliable, we conducted a replication study with a different group of participants in Experiment 2.

Experiment 2

Methods.

Participants.

A power analysis in G-Power (Faul, Erdfelder, Lang, & Buchner, 2007) indicated that, in order to have sufficient power (95%) to detect an effect size of $d=.83$ (i.e., the average effect size

observed for the congruency effect using paired-samples t-tests, averaged across left and right prisms) with $p=.05$, a sample size of $n=21$ was required. Therefore, for Experiment 2 we recruited a new sample of 25 healthy undergraduate students from MacEwan University (mean age=21.29 years; SD=5.94; 12 males). Participants provided written informed consent and were compensated with either course credit, or \$10 per hour of participation. All experimental procedures were approved by the MacEwan University Research Ethics Board.

Experimental setup and procedure.

As this was a replication study, the setup and procedure for Experiment 2 were identical to those described in Experiment 1, and for control participants in Striemer and colleagues (2019) with the only difference being that we replaced the 2cm reversing checkerboard stimulus, with a circular target 2cm in diameter. The outline of the target appeared on the touch screen for 1 sec and then was filled in. Once the target filled in a 1000Hz tone indicated that the participant was to reach out and touch the target as quickly and accurately as possible with their index finger.

Results.

We analyzed the data using the same general strategy outlined in Experiment 1. However, since Experiment 2 was a replication study, we used planned comparisons to directly examine the effect of hand (left vs. right), at each level of prism shift (left shift vs. right shift), for each of the dependent measures.

Target directed pointing (TDP) and washout pointing.

All target directed pointing (TDP) and washout pointing data for Experiment 2 are reported in Figure 5a and Supplementary Table 3. First, we confirmed that participants were able to adapt to prisms in the expected direction for each hand (left vs. right) by prism shift (left vs. right) combination by comparing the average endpoint error for the 20 baseline TDP trials to the average endpoint error for the first 5 trials during the washout phase post PA, using paired-samples t-tests. This analysis revealed that participants were able to adapt in the expected direction for each hand by prism shift combination. Specifically, participants were able to adapt to left prisms with the left (pre= -.17cm vs. post=1.78cm; $t(24)=8.83$, $p<.001$) and the right hand (pre= .14cm vs. post=1.54cm; $t(24)=3.99$, $p<.001$). Participants were also able to adapt to right prisms with the left (pre= .18cm vs. post= -1.73cm; $t(24)=7.93$, $p<.001$) and the right hand (pre=.42cm vs. post= -1.69cm; $t(24)=6.55$, $p<.001$).

Next, we wanted to examine whether there was any difference in the magnitude of aftereffects induced for each hand by prism shift combination as measured by washout pointing. To measure this, we calculated the absolute difference in aftereffect for each hand by prism shift combination by subtracting the average pointing error from the 20 baseline TDP trials from the average pointing error for the first 5 washout trials post PA. A hand (left vs. right) by prism shift (left shift vs. right shift) ANOVA revealed no main effects, but a marginal hand x prism shift interaction ($F(1,24)=4.02$, $p=.056$, $\eta^2_p=.14$). To further analyze these data, we used planned comparisons to examine the simple main effect of hand at each level of prism shift. There was no significant difference in aftereffect between the two hands for left prisms (left hand=1.95cm vs. right hand=1.72cm; $F(1)=1.25$, $p=.28$). However, there was a significant difference in aftereffect between the two hands for right prisms (left hand=1.91cm vs. right hand=2.29cm; $F(1)=5.46$,

$p=.028$) such that the aftereffect was larger when the hand and the prism shift were congruent (right hand, right prisms) vs. incongruent (left hand, right prisms).

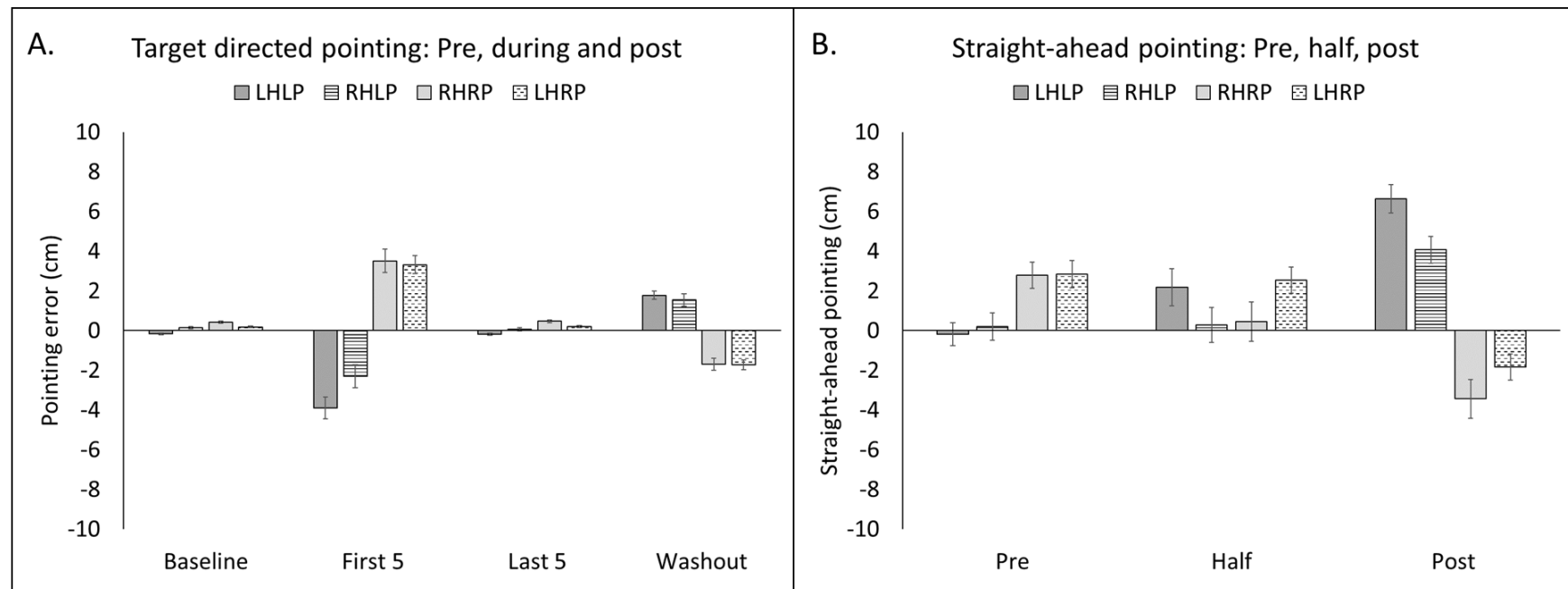
We then examined the magnitude of initial pointing errors during the PA phase by calculating the absolute difference in pointing error for the average of the first five pointing trials during PA and the average of the 20 baseline trials completed prior to PA. A hand (left vs. right) by prism shift (left shift vs. right shift) ANOVA revealed no main effects, but a significant hand x prism shift interaction ($F(1,24)=6.10$, $p=.021$, $\eta^2_p=.20$). To further analyze the interaction, we used planned comparisons examining the simple main effect of hand for each level of prism shift. This analysis revealed a significant difference in initial TDP error between the two hands for left prisms such that the initial pointing error was somewhat larger when the hand and prism shift were congruent (left hand, left prisms=3.75cm), compared to incongruent (right hand, left prisms=3.11cm; $F(1)=4.55$, $p=.043$). However, there was no significant difference in initial TDP error between the two hands for right prisms (left hand=3.27cm vs. right hand=3.53cm; $F(1)=.65$, $p=.43$).

Finally, we examined pointing error reduction by calculating the absolute difference in pointing errors for the average of the first 5 trials with prisms on, and the average pointing error for the last 5 trials with prisms on. A hand (left vs. right) by prism shift (left vs. right) ANOVA revealed no main effects, but a marginal hand x prism shift interaction ($F(1,24)=4.21$, $p=.052$, $\eta^2_p=.15$). Using planned comparisons, we then examined the simple main effect of hand for each level of prism shift. The analysis indicated that there was a significant difference in pointing error reduction between the two hands for left prisms such that pointing error reduction was greater when the hand and direction of prism shift were congruent (i.e., left hand, left prism=3.75cm) compared to incongruent (right hand, left prism=3.03cm; $F(1)=4.47$, $p=.045$).

However, there was no difference in pointing error reduction between the two hands for right prisms (left hand=3.27cm vs. right hand=3.50cm; $F(1)=.25$, $p=.63$).

--insert Figure 5 here--

Figure 5. A) Average pointing error (in cm) for Experiment 2 for the target directed pointing task at baseline, as well as for the first five trials during prism adaptation (First 5), the last five trials during prism adaptation (Last 5) and the first five trials of the Washout phase following adaptation (Washout). Note that during the first five trials during adaptation, the participant misses in the direction of the prism shift. However, by the last five trials during adaptation, the participant has significantly reduced their pointing errors. An aftereffect is demonstrated during the washout phase when the prisms are removed, and the participant now reaches in the direction opposite the prism shift. **B)** Average straight-ahead pointing (SAP) data (in cm) for Experiment 2 pre, halfway, and post adaptation. For SAP, aftereffects are demonstrated when the participant reaches in the direction opposite the prism shift halfway and/or post adaptation. For both Figures, positive values are to the right of center, negative values are to the left of center. Error bars represent the standard error.



Straight-ahead pointing (SAP).

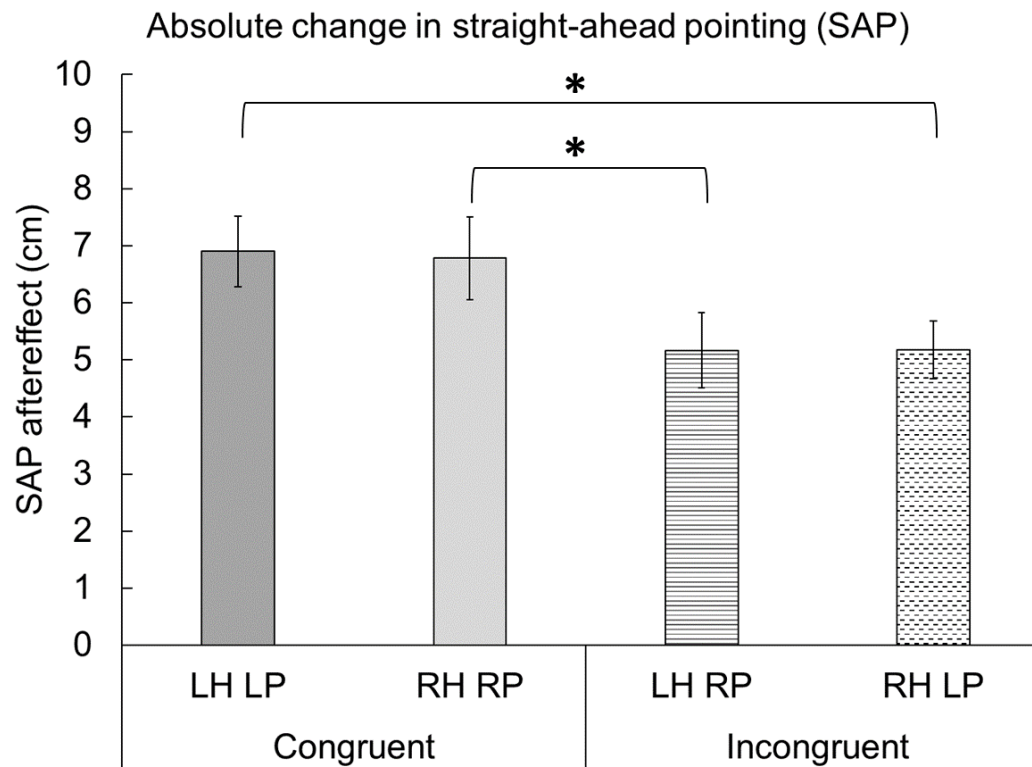
The straight-ahead pointing (SAP) data for Experiment 2 are presented in Figure 5b and Supplementary Table 4. First, we wanted to ensure that participants were able to adapt to each hand (left vs. right) by prism shift (left shift vs. right shift) combination. To analyze this, we ran separate one-way ANOVAs for each hand by prism shift combination with time (pre vs. post vs. final) as the within-subject factor. This analysis demonstrated that participants were able to successfully adapt to prisms in the expected direction for each hand x prism shift combination (all F 's > 12.08 , all p 's $< .001$). However, subsequent Holm-corrected post-hoc tests indicated that the temporal profile of adaptation differed depending on which hand by prism shift combination was examined. Specifically, when the hand used and the direction of prism shift were congruent, SAP at each time point was significantly different from each other in the expected direction. This was true for both the left hand, left prism (pre SAP = $-.19\text{cm}$ vs. halfway SAP = 2.18cm vs. post SAP = 6.63cm ; all t 's > 3.13 , all p 's $< .003$) and right hand, right prism conditions (pre SAP = 2.79cm vs. halfway SAP = 0.44cm vs. post SAP = -3.44cm ; all t 's > 2.94 , all p 's $< .005$). In contrast, when the hand and prism shift were incongruent, participants required the full 200 adaptation TDP trials to demonstrate a significant shift in SAP in the expected direction. This was true for both the left hand, right prism condition (pre SAP = 2.83cm vs. halfway SAP = 2.55cm ($t(24) = .42$, $p = .68$); pre SAP vs. post SAP = -1.83cm ; $t(24) = 6.83$, $p < .001$) as well as the right hand, left prism condition (pre SAP = $.20\text{cm}$ vs. halfway SAP = $.29\text{cm}$; ($t(24) = .10$, $p = .92$); pre SAP vs. post SAP = 4.07 ; $t(24) = 4.30$, $p < .001$).

After establishing that participants were able to successfully adapt in each condition, we then wanted to examine if there were any differences in the magnitude of SAP aftereffects as a function of hand used and direction of prism shift. To examine this, we calculated the absolute

difference in SAP by subtracting mean pre SAP from mean post SAP for each hand by prism shift combination. A hand (left vs. right) by prism shift (left shift, right shift) ANOVA revealed no main effects, but a significant hand x prism shift interaction ($F(1,24)=7.80$, $p=.01$, $\eta^2_p=.25$). Using planned comparisons, we once again examined the simple main effect of hand at each level of prism shift. Similar to the results of Experiment 1, this analysis indicated that the magnitude of SAP aftereffects was significantly larger when the hand and the direction of prism shift were congruent compared to incongruent (Figure 6). This was true for both left prisms (left hand=6.90cm vs. right hand=5.18cm; $F(1)=5.28$, $p=.031$) and right prisms (left hand=5.17cm vs. right hand=6.79cm; $F(1)=5.22$, $p=.031$).

--Insert Figure 6 here--

Figure 6. Depicts the absolute change in straight-ahead pointing (SAP) pre vs. post prism adaptation from the replication study carried out in Experiment 2. Data are presented as a function of hand used (left hand=LH, right hand=RH) and direction of prism shift (leftward shifting prisms=LP, rightward shifting prisms=RP). Data are depicted in centimeters (cm). Error bars represent the standard error. * indicates $p < .05$.



Comparing the congruency effects between Experiment 1 and Experiment 2.

Finally, we directly compared the magnitude of the congruency effects obtained for SAP in Experiments 1 and 2 using a mixed-model ANOVA with hand (left vs. right) and prism shift (left shift vs. right shift) as within-subjects factors and “experiment” (Experiment 1 vs. 2) as a between-subject factor. This analysis revealed no main effects of hand ($F(1,40)=0.22$, $p=.64$) or prism shift ($F(1,40)=0.30$, $p=.59$). Consistent with the results reported in Experiments 1 & 2, there was a significant hand x prism shift interaction ($F(1,40)=23.14$, $p<.001$, $\eta^2_p=.37$). A simple main effects analysis revealed that the magnitude of the aftereffects observed for SAP were larger when the hand used to adapt and the direction of prism shift were congruent vs. incongruent for both left prisms (left hand=6.37cm vs. right hand=3.93cm; $F(1)=19.67$, $p<.001$) and for right prisms (left hand=4.31cm vs. right hand=6.45cm; $F(1)=12.80$, $p<.001$).

In addition, there was a main effect of the between-subject variable “experiment” ($F(1,40)=10.05$, $p=.003$, $\eta^2_p=.20$) such that, overall, the absolute magnitude of the aftereffects observed in Experiment 2 (6.19cm) were larger than Experiment 1 (4.34cm). However, there were no interactions involving the between-subject factor of “experiment” (all p ’s $>.20$).

Discussion

In the current study we examined whether PA aftereffects were influenced by the combination of the hand used to adapt (left vs. right), and the direction of the visual shift (left vs. right). In Experiment 1, using a re-analysis of healthy control data ($n=17$) from a previously published study (Striemer, Enns, et al., 2019), we observed a significant “congruency effect” such that the magnitude of prism aftereffects, as measured by SAP, were larger when the hand used to adapt and the direction of visual shift were congruent (e.g., right hand, right prisms) compared to

incongruent (e.g., left hand, right prisms). However, the congruency effect was not observed for initial prism pointing error, pointing error reduction, or “washout” pointing where participants pointed to visible targets following PA.

Importantly, we replicated the congruency effect for SAP in Experiment 2 in a separate group of participants ($n=25$). In addition, the SAP results from Experiment 2 also provided some evidence for the temporal evolution of the congruency effect. That is, for congruent adaptation conditions (i.e., left hand, left prisms and right hand, right prisms), participants were significantly adapted when SAP was measured halfway through adaptation, after only 100 pointing trials. In contrast, no significant aftereffects were present for SAP for incongruent adaptation conditions (i.e., right hand, left prisms or left hand, right prisms) until the full set of 200 pointing trials had been completed. Furthermore, in Experiment 2 we also found some evidence for a partial congruency effect for “washout” pointing such that aftereffects were larger when adapting to right prisms with the right compared to the left hand. In addition, for initial prism pointing error, and pointing error reduction, the effects were somewhat larger when adapting to left prisms with the left, but not the right hand. Finally, a direct comparison between the two studies indicated that the size of the congruency effect did not differ between the two Experiments.

In summary, data across two experiments demonstrates that when the hand used to adapt and the direction of visual shift were congruent (i.e., left hand, left prisms or right hand, right prisms), it led to significantly larger aftereffects compared to incongruent adaptation conditions (i.e., left hand, right prisms or right hand, left prisms). Our results are partially supported by the behavioral data from a recent neuroimaging study by Farron and colleagues (Farron, Clarke, & Crottaz-Herbette, 2022) in which they observed larger PA aftereffects when participants adapted

to rightward shifting prisms with the right hand (congruent), compared to rightward shifting prisms with the left hand (incongruent). Unfortunately, they did not test both hands with leftward shifting prisms.

In the current study, we observed the most consistent evidence for the congruency effect for SAP which primarily measures changes in sensed arm position, compared to “washout” pointing, where the participant can see their reaching hand and target, and thus is thought to index a combination of both visual and proprioceptive adaptation (Redding et al., 2005; Redding & Wallace, 1988). Furthermore, in the current study we used a concurrent adaptation condition (i.e., with view of the reaching hand) which is known to result in larger changes in sensed arm position, compared a to terminal feedback condition (i.e., no view of the reaching hand), which is known to result in larger changes in sensed eye position (Herlihey, Black, & Ferber, 2012; Redding et al., 2005; Redding & Wallace, 1988). Given this, it seems reasonable to assume that the congruency effect might be more related to proprioceptive changes in sensed arm position, rather than eye position.

It is worth noting that a previous study by Redding and Wallace (2009) examined the inter-manual transfer of PA aftereffects when adapting to leftward or rightward shifting prisms with the left or the right hand. However, they used a terminal feedback condition which, again, is known to result in larger changes in sensed eye compared to arm position (Redding et al., 2005; Redding & Wallace, 1988). In addition, Redding and Wallace (2009) only reported a combined measure of eye (visual) and limb (arm) proprioceptive shift, and not arm proprioceptive shift alone. Given the differences in adaptation procedures, and aftereffect measures reported, it is difficult to directly compare our two studies.

Future studies should examine whether the congruency effect can also be observed for measures of visual adaptation, such as visual straight-ahead, where the participant must indicate when a horizontally moving target is aligned with their nose (Herlihey et al., 2012; Redding et al., 2005; Redding & Wallace, 1988). In addition, future studies could examine whether the congruency effect is altered based on the type of visual feedback that is used during adaptation. If the congruency effect is primarily driven by proprioceptive changes in sensed arm position, then one would predict that the effect would be absent or reduced for measures of visual adaptation, and/or when terminal feedback conditions are used during adaptation.

What might explain the congruency effect?

As mentioned earlier, in the cerebral cortex sensory inputs (i.e., both visual and proprioceptive) and motor outputs from the same side are processed, at least initially, in the same (contralateral) hemisphere (Kolb & Whishaw, 2009; Nolte, 2002). This is consistent with neuroimaging studies which demonstrate increased activation in the PPC contralateral to the reaching hand during visually guided reaching and grasping (for a review see Culham, Cavina-Pratesi, & Singhal, 2006). Given that reaches are coded relative to gaze position (Batista, Buneo, Snyder, & Andersen, 1999; Buneo & Andersen, 2006; Dijkerman et al., 2006; Khan et al., 2005), then, for a participant who is adapting to rightward shifting prisms with the right hand, visual inputs from the right visual field, proprioceptive inputs from the right arm, and motor commands to control the right arm, would all be processed (initially) in the left hemisphere. Likewise, when adapting to leftward shifting prisms with the left hand, visual inputs from the left visual field, proprioceptive inputs from the left arm, and motor commands to control the left arm, would all be processed (initially) in the right hemisphere. It could be the case that, during these congruent

adaptation conditions, the visual and/or proprioceptive error signals that are generated when a participant mis-reaches during PA are integrated more efficiently (as measured by increased aftereffects) when all the necessary signals (visual, proprioceptive, motor) are processed within the same cerebral hemisphere.

In contrast, during incongruent adaptation conditions, such as adapting to leftward shifting prisms with the right hand, the visual inputs from the left visual field would arrive in the right hemisphere, whereas the proprioceptive inputs from the right arm, and the motor commands to control the right arm would be processed in the left hemisphere. The opposite would be true when adapting to right prisms with the left hand. It could be the case that it is more difficult to integrate visual and/or proprioceptive error signals generated during adaptation when they are processed in opposite cerebral hemispheres which, ultimately, could lead to less optimal adaptation. This is consistent with the fact that patients with lesions to the PPC – a region critical for computing visuomotor transformations (for reviews see Andersen, Andersen, Hwang, & Hauschild, 2014; Buneo & Andersen, 2006; Freedman & Ibos, 2018) – often have more difficulty adapting to prisms that shift vision towards the contralesional (but not the ipsilesional) side (e.g., Rossetti et al., 1998; Striemer, Enns, et al., 2019).

Alternatively, the congruency effect may arise through similar mechanisms within the cerebellum. As noted earlier, the cerebellum is known to play an important role in PA, and motor learning in general (e.g., Baizer et al., 1999; Bossom, 1965; Martin et al., 1996; Norris et al., 2011; Pisella et al., 2005; Weiner et al., 1983; Welch & Goldstein, 1972; Werner et al., 2010). One prominent theory suggests that the cerebellum receives efference copies of motor commands in order to create a “forward model” to predict the sensory consequences of an action (for a recent review see Sokolov, Miall, & Ivry, 2017). If the sensory prediction generated by the

cerebellum does not match the actual outcome of the movement based on visual and proprioceptive feedback – as is the case when a participant mis-reaches with prisms on – then this generates a sensory prediction error (Sokolov et al., 2017). Through an iterative learning process over many trials, sensory prediction errors can then be used to update the forward model for subsequent reaches, in order to reduce the discrepancy between the desired movement, and the actual movement (Sokolov et al., 2017).

It is well known that the cerebellum exerts ipsilateral control over the limbs, such that unilateral lesions to the cerebellum will affect movements on the same side (Holmes, 1917; Nolte, 2002). Interestingly, a recent fMRI study demonstrated that the cerebellum also receives only ipsilateral visual inputs, such that the left cerebellum receives input from the left visual field and vice-versa (van Es, van der Zwaag, & Knapen, 2019). Importantly, there are very few white matter fibers connecting homotopic regions between the two cerebellar hemispheres (Jenkins, 2000). This means that, unlike the cerebral cortex, information that arrives in one cerebellar hemisphere is processed largely within that hemisphere, with little direct influence from the other cerebellar hemisphere. Given that each cerebellar hemisphere controls the ipsilateral limb, and receives primarily ipsilateral proprioceptive (Nolte, 2002) and visual inputs (van Es et al., 2019), then if a participant is adapting to rightward shifting prisms with their right hand (i.e., a congruent adaptation condition) visual inputs from the right visual field, proprioceptive inputs from the right arm, and motor outputs to control the right arm, would all be processed in the (ipsilateral) right cerebellum. In contrast, in an incongruent adaptation condition – such as adapting to rightward shifting prisms with the left hand – input from the right visual field would arrive in the right cerebellum, whereas proprioceptive inputs from the left arm, and motor commands to control the right arm, would come from the left cerebellum. Thus, it may be the

case that the visual and/or proprioceptive error signals generated during PA may be integrated more efficiently (as indexed by increased aftereffects) when they are processed in the same (ipsilateral) cerebellar hemisphere in congruent PA conditions, as opposed to opposite cerebellar hemispheres, as would be the case for incongruent adaptation conditions.

Data from a single-case study by Pisella and colleagues (Pisella et al., 2005) supports this cerebellar hypothesis. In this study, a patient with a left cerebellar lesion was adapted to leftward or rightward shifting prisms with the left or the right hand. Their results demonstrated that the patient was able to adapt to rightward shifting prisms with either hand, but was unable to adapt to leftward shifting prisms with either hand. That is, when the visual input from the rightward shifting prisms was processed in the intact right cerebellar hemisphere, the patient was able to adapt successfully. However, when the visual input from the leftward shifting prisms was processed in the damaged left cerebellar hemisphere, the patient was not able to adapt. It is also interesting to note that, consistent with the current results, the patient appears to demonstrate a larger aftereffect for the congruent adaptation condition (right hand, right prisms), compared to the incongruent adaptation condition (left hand, right prisms), although this was not directly tested by Pisella and colleagues (see Figure 2 in Pisella et al., 2005).

In conclusion, in the current study we have presented evidence in favour of a congruency effect during PA. We have argued that this congruency effect may be linked with a more efficient integration of sensory error signals that arise during PA when they are processed in the same cerebral or cerebellar hemisphere – as is the case for congruent adaptation conditions – compared to opposite hemispheres – as is the case for incongruent adaptation conditions. Whether the neural processes that result in the congruency effect arise in the PPC and/or the cerebellum is an important question for future research. Ultimately, a better understanding of the

cognitive and neural mechanisms underlying the congruency effect will help us build more precise models of visuomotor learning, and may allow us to develop more effective applications of PA for treating patients with attentional disorders following brain damage (e.g., Pisella et al., 2006; Rossetti et al., 1998; Striemer & Danckert, 2010).

Acknowledgements:

This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (2022-03608) awarded to Christopher Striemer. The authors would like to thank Brittany Angus-Cook for her assistance with data collection.

Conflict of interest statement:

On behalf of all authors, the corresponding author states that there is no conflict of interest.

Data availability statement:

The authors confirm that the summarized group data supporting the findings of this study are available within the article or its Supplementary Material. Raw data and individual participant data cannot be made available because of ethical restrictions. Specifically, all participants in the study signed a consent form which indicated that only the researchers involved in the study would have access to individual participant data. Requests for access to individual participant data must be submitted to the corresponding author, and data sharing agreements must be submitted to MacEwan University Research Office.

References:

- Andersen, R. A., Andersen, K. N., Hwang, E. J., & Hauschild, M. (2014). Optic ataxia: from Balint's syndrome to the parietal reach region. *Neuron*, 81(5), 967-983.
- Arcaro, M. J., Thaler, L., Quinlan, D. J., Monaco, S., Khan, S., Valyear, K. F., . . . Culham, J. C. (2018). Psychophysical and neuroimaging responses to moving stimuli in a patient with the Riddoch phenomenon due to bilateral visual cortex lesions. *Neuropsychologia*. doi:10.1016/j.neuropsychologia.2018.05.008
- Baizer, J. S., Kralj-Hans, I., & Glickstein, M. (1999). Cerebellar lesions and prism adaptation in macaque monkeys. *Journal of Neurophysiology*, 81(4), 1960-1965. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=10200230
- Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach plans in eye-centered coordinates. *Science*, 285(5425), 257-260.
- Bossom, J. (1965). The effect of brain lesions on prism-adaptation in monkey. *Psychonomic Science*, 2(1-12), 45-46.
- Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, 44(13), 2594-2606. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=16300804
- Chapman, H. L., Eramudugolla, R., Gavrilescu, M., Strudwick, M. W., Loftus, A., Cunningham, R., & Mattingley, J. B. (2010). Neural mechanisms underlying spatial realignment during adaptation to optical wedge prisms. *Neuropsychologia*, 48(9), 2595-2601. doi:10.1016/j.neuropsychologia.2010.05.006
- Clower, D. M., Hoffman, J. M., Votaw, J. R., Faber, T. L., Woods, R. P., & Alexander, G. E. (1996). Role of posterior parietal cortex in the recalibration of visually guided reaching. *Nature*, 383(6601), 618-621. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=8857536
- Colent, C., Pisella, L., Bernieri, C., Rode, G., & Rossetti, Y. (2000). Cognitive bias induced by visuo-motor adaptation to prisms: a simulation of unilateral neglect in normal individuals? *Neuroreport*, 11(9), 1899-1902. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=10884040
- Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: what have we learned from neuroimaging? *Neuropsychologia*, 44(13), 2668-2684. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=16337974
- Danckert, J., Ferber, S., & Goodale, M. A. (2008). Direct effects of prismatic lenses on visuomotor control: an event-related functional MRI study. *European Journal of Neuroscience*, 28(8), 1696-1704. doi:EJN6460 [pii]10.1111/j.1460-9568.2008.06460.x
- Dijkerman, H. C., McIntosh, R. D., Anema, H. A., de Haan, E. H., Kappelle, L. J., & Milner, A. D. (2006). Reaching errors in optic ataxia are linked to eye position rather than head or body position. *Neuropsychologia*, 44(13), 2766-2773. Retrieved from

- http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=16321407
- Farron, N., Clarke, S., & Crottaz-Herbette, S. (2022). Does hand modulate the reshaping of the attentional system during rightward prism adaptation? An fMRI study. *Front Psychol*, 4392.
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior research methods*, 39(2), 175-191.
- Freedman, D. J., & Ibos, G. (2018). An integrative framework for sensory, motor, and cognitive functions of the posterior parietal cortex. *Neuron*, 97(6), 1219-1234.
- Herlihey, T. A., Black, S. E., & Ferber, S. (2012). Terminal, but not concurrent prism exposure produces perceptual aftereffects in healthy young adults. *Neuropsychologia*, 50(12), 2789-2795. doi:S0028-3932(12)00348-X [pii]10.1016/j.neuropsychologia.2012.08.009
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*, 65-70.
- Holmes, G. (1917). The symptoms of acute cerebellar injuries due to gunshot injuries. *Brain*, 40(4), 461-535.
- JASP-Team. (2022). JASP (version 0.16.3)[computer software].
- Jenkins, J. R. (2000). *Atlas of neuroradiologic embryology, anatomy, and variants*: Lippincott Williams & Wilkins.
- Khan, A. Z., Pisella, L., Vighetto, A., Cotton, F., Luaute, J., Boisson, D., . . . Rossetti, Y. (2005). Optic ataxia errors depend on remapped, not viewed, target location. *Nature Neuroscience*, 8(4), 418-420. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15768034
- Kolb, B., & Whishaw, I. Q. (2009). *Fundamentals of human neuropsychology*: Macmillan.
- Luaute, J., Schwartz, S., Rossetti, Y., Spiridon, M., Rode, G., Boisson, D., & Vuilleumier, P. (2009). Dynamic changes in brain activity during prism adaptation. *Journal of Neuroscience*, 29(1), 169-178. doi:29/1/169 [pii]10.1523/JNEUROSCI.3054-08.2009
- Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996). Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain*, 119 (Pt 4), 1183-1198. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=8813282
- Michel, C., Pisella, L., Halligan, P. W., Luaute, J., Rode, G., Boisson, D., & Rossetti, Y. (2003). Simulating unilateral neglect in normals using prism adaptation: implications for theory. *Neuropsychologia*, 41(1), 25-39. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=12427563
- Michel, C., Vernet, P., Courtine, G., Ballay, Y., & Pozzo, T. (2008). Asymmetrical after-effects of prism adaptation during goal oriented locomotion. *Experimental Brain Research*, 185, 259-268.
- Mutha, P. K., Sainburg, R. L., & Haaland, K. Y. (2011). Left parietal regions are critical for adaptive visuomotor control. *Journal of Neuroscience*, 31(19), 6972-6981.

- Nolte, J. (2002). *The Human Brain: An Introduction to its Functional Anatomy* (5th ed.). St. Louis: Mosby, Inc.
- Norris, S. A., Hathaway, E. N., Taylor, J. A., & Thach, W. T. (2011). Cerebellar inactivation impairs memory of learned prism gaze-reach calibrations. *Journal of Neurophysiology*, 105(5), 2248-2259. doi:10.1152/jn.01009.2010
- Pisella, L., Michel, C., Grea, H., Tilikete, C., Vighetto, A., & Rossetti, Y. (2004). Preserved prism adaptation in bilateral optic ataxia: strategic versus adaptive reaction to prisms. *Experimental Brain Research*, 156(4), 399-408. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15133651
- Pisella, L., Rode, G., Farné, A., Tilikete, C., & Rossetti, Y. (2006). Prism adaptation in the rehabilitation of patients with visuo-spatial cognitive disorders. *Current Opinion in Neurology*, 19(6), 534-542. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=17102690
- Pisella, L., Rossetti, Y., Michel, C., Rode, G., Boisson, D., Pelisson, D., & Tilikete, C. (2005). Ipsidirectional impairment of prism adaptation after unilateral lesion of anterior cerebellum. *Neurology*, 65(1), 150-152. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=16009906
- Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: a tutorial in theory and method. *Neuroscience and Biobehavioral Reviews*, 29(3), 431-444. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15820548
- Redding, G. M., & Wallace, B. (1988). Components of prism adaptation in terminal and concurrent exposure: Organization of the eye-hand coordination loop. *Perception & Psychophysics*, 44(1), 59-68.
- Redding, G. M., & Wallace, B. (2006). Prism adaptation and unilateral neglect: review and analysis. *Neuropsychologia*, 44(1), 1-20. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=15907951
- Redding, G. M., & Wallace, B. (2009). Asymmetric visual prism adaptation and intermanual transfer. *Journal of motor behavior*, 41(1), 83-96.
- Reed, S. A., & Dassonville, P. (2014). Adaptation to leftward-shifting prisms enhances local processing in healthy individuals. *Neuropsychologia*, 56, 418-427.
- Rossetti, Y., Rode, G., Pisella, L., Farné, A., Li, L., Boisson, D., & Perenin, M. T. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, 395(6698), 166-169. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=9744273
- Sokolov, A. A., Miall, R. C., & Ivry, R. B. (2017). The Cerebellum: Adaptive Prediction for Movement and Cognition. *Trends in Cognitive Science*, 21(5), 313-332. doi:10.1016/j.tics.2017.02.005
- Striener, C. L., & Danckert, J. (2010). Through a prism darkly: re-evaluating prisms and neglect. *Trends in Cognitive Science*, 14(7), 308-316. doi:S1364-6613(10)00073-2 [pii]

- 10.1016/j.tics.2010.04.001
- Striemer, C. L., Enns, J. T., & Whitwell, R. L. (2019). Visuomotor adaptation in the absence of input from early visual cortex. *Cortex*, 115, 201-215. doi:10.1016/j.cortex.2019.01.022
- Striemer, C. L., Whitwell, R. L., & Goodale, M. A. (2019). Affective blindsight in the absence of input from face processing regions in occipital-temporal cortex. *Neuropsychologia*, 128, 50-57. doi:10.1016/j.neuropsychologia.2017.11.014
- van Es, D. M., van der Zwaag, W., & Knapen, T. (2019). Topographic Maps of Visual Space in the Human Cerebellum. *Current Biology*, 29(10), 1689-1694 e1683. doi:10.1016/j.cub.2019.04.012
- Von Helmholtz, H. (1867). *Handbuch der physiologischen Optik* (Vol. 9): Voss.
- Weiner, M. J., Hallett, M., & Funkenstein, H. H. (1983). Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. *Neurology*, 33(6), 766-772. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=6682520
- Welch, R. B., & Goldstein, G. (1972). Prism adaptation and brain damage. *Neuropsychologia*, 10(4), 387-394. Retrieved from http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=PubMed&dopt=Citation&list_uids=4348505
- Werner, S., Bock, O., Gizewski, E. R., Schoch, B., & Timmann, D. (2010). Visuomotor adaptive improvement and aftereffects are impaired differentially following cerebellar lesions in SCA and PICA territory. *Experimental Brain Research*, 201(3), 429-439. doi:10.1007/s00221-009-2052-6

Supplementary Material

Supplementary Table 1: Mean target directed pointing (TDP) data from Experiment 1 (n=17) as a function of hand (left vs. right) and direction of prism shift (left vs. right). All data are reported in centimeters (cm). Standard deviation (SD) is reported in brackets. Negative values are to the left of center, positive values are to the right of center. Data are re-analysis of control participants from Striemer et al., 2019.

Condition	Baseline (pre) prisms pointing	First 5 trials with prisms on	Last 5 trials with prisms on	Washout pointing
Left hand, left prisms	-.42 (.65)	-7.03 (3.89)	-.58 (.68)	3.14 (1.93)
Right hand, left prisms	-.12 (.43)	-5.05 (3.07)	.001 (1.07)	2.41 (2.13)
Left hand, right prisms	.11 (.45)	6.86 (3.30)	.14 (.58)	-3.93 (2.4)
Right hand, right prisms	.44 (.46)	6.89 (2.89)	.56 (.48)	-3.04 (2.28)

Supplementary Table 2: Mean straight-ahead pointing (SAP) data from Experiment 1 (n=17) as a function of hand (left vs. right) and direction of prism shift (left vs. right). All data are reported in centimeters (cm). Standard deviation (SD) is reported in brackets. Negative values are to the left of center, positive values are to the right of center. Data are re-analysis of control participants from Striemer et al., 2019.

Condition	Baseline (pre) SAP	Halfway SAP	Post SAP
Left hand, left prisms	-.74 (1.82)	4.86 (2.62)	4.73 (2.44)
Right hand, left prisms	-1.65 (3.25)	-.13 (3.66)	.13 (3.40)
Left hand, right prisms	2.81 (2.60)	.68 (4.66)	.80 (3.23)
Right hand, right prisms	1.90 (3.22)	-4.13 (3.49)	-3.85 (3.53)

Supplementary Material

Supplementary Table 3. Mean target directed pointing (TDP) data from Experiment 2 (n=25) as a function of hand (left vs. right) and direction of prism shift (left vs. right). All data are reported in centimeters (cm). Standard deviation (SD) is reported in brackets. Negative values are to the left of center, positive values are to the right of center.

Condition	Baseline (pre) prisms pointing	First 5 trials with prisms on	Last 5 trials with prisms on	Washout pointing
Left hand, left prisms	-.17 (.21)	-3.90 (2.78)	-.19 (.29)	1.78 (1.05)
Right hand, left prisms	.14 (.30)	-2.31 (2.90)	.07 (.39)	1.54 (1.60)
Left hand, right prisms	.18 (.32)	3.32 (2.31)	.19 (.28)	-1.73 (1.25)
Right hand, right prisms	.42 (.24)	3.51 (2.92)	.47 (.36)	-1.69 (1.49)

Supplementary Table 4: Mean straight-ahead pointing (SAP) data from Experiment 2 (n=25) as a function of hand (left vs. right) and direction of prism shift (left vs. right). All data are reported in centimeters (cm). Standard deviation (SD) is reported in brackets. Negative values are to the left of center, positive values are to the right of center.

Condition	Baseline (pre) SAP	Halfway SAP	Post SAP
Left hand, left prisms	-.19 (2.92)	2.18 (4.73)	6.63 (3.53)
Right hand, left prisms	.20 (3.40)	.28 (4.41)	4.07 (3.40)
Left hand, right prisms	2.83 (3.43)	2.55 (3.27)	-1.83 (3.32)
Right hand, right prisms	2.79 (3.31)	.44 (4.93)	-3.44 (4.94)