Prism Adaptation Magnitude Has Differential Influences on Perceptual vs. Manual Responses

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Abstract:

Previous research has indicated that rightward prism adaptation can reduce symptoms of spatial neglect following right brain damage. In addition, leftward prism adaptation can create “neglect-like” patterns of performance in healthy adults on tasks that measure attention and spatial biases. Although a great deal of research has focused on which behaviours are influenced by prism adaptation, very few studies have focused directly on how the magnitude of visual shift induced by prisms might be related to the observed aftereffects, or the effects of prisms on measures of attentional and spatial biases. In the current study we examined these questions by having groups of healthy adult participants complete manual line bisection and landmark tasks prior to and following adaptation to either 8.5° (15 diopter; n=22) or 17° (30 diopter; n=25) leftward shifting prisms. Our results demonstrated a significantly larger rightward shift in straight-ahead pointing (a measure of prism aftereffect) following adaptation to 17°, compared to 8.5° leftward shifting prisms. In addition, only 17° leftward shifting prisms resulted in a significant rightward shift in line bisection following adaptation. However, there was a significant change in performance on the landmark task pre vs. post adaptation in both the 8.5° and 17° leftward shifting prisms groups. Interestingly, correlation analyses indicated that changes in straight-ahead pointing pre vs. post adaptation were positively correlated with changes in performance on the manual line bisection task, but not the landmark task. These data suggest that larger magnitudes of prism adaptation seem to have a greater influence on tasks that require a response with the adapted hand (i.e., line bisection), compared to tasks that only require a perceptual judgment (i.e., the landmark task). In addition, these data provide further evidence that the effects of prisms on manual and perceptual responses are not related to one-another.

Keywords: prism adaptation, neglect, pseudoneglect, line bisection, visual attention

Introduction:

Damage to the right temporo-parietal cortex often leads to spatial neglect, a disorder in which patients are unable to attend to people or objects on the contralesional side (Husain & Rorden, 2003; Karnath, Ferber, & Himmelbach, 2001; Karnath, Fruhmann Berger, Kuker, & Rorden, 2004; Karnath & Rorden, 2012; Mort et al., 2003; Vallar & Perani, 1986). Neglect is quite common post-stroke occurring in approximately 50% of patients with right hemisphere brain damage (Buxbaum et al., 2004); however, right spatial neglect can also occur following left hemisphere stroke (Kleinman et al., 2007). In addition, the presence of neglect post-stroke is also a significant predictor for a poorer functional recovery (Cherney & Halper, 2001). Therefore, the development of methods to help reduce the symptoms of neglect is of great clinical significance.

One method that is effective for reducing symptoms of neglect is the prism adaptation (PA) technique that was developed by Rossetti and colleagues (Pisella, Rode, Farné, Tilikete, & Rossetti, 2006; Rossetti et al., 1998). Prior to PA, if you ask a patient to point straight-ahead from their body midline without visual feedback the patient typically points far to the right because neglect induces a rightward shift in the egocentric reference frame (Karnath, Niemeier, & Dichgans, 1998; Karnath & Perenin, 1998). During PA patients are asked to wear glasses that shift their vision rightwards (typically a 10° shift is used). While wearing the prisms the patient is asked to reach towards targets located to the left and right of their body midline. Initially when the patient reaches to the target they miss far to the right because of the visual shift induced by the prisms; however, after a few reaches they learn to adjust their movements leftward to compensate for the rightward visual shift. Following PA the patient is again asked to point straight-ahead without visual feedback. Because the patient had to adjust their movements leftward to compensate for the rightward visual shift, their judgments of straight-ahead also shift significantly leftward, closer to true center (Pisella et al., 2006; Rossetti et al., 1998). In addition, this leftward shift in the egocentric reference frame also induces a significant leftward shift in exploratory motor behaviours which leads to improved performance on clinical measures of neglect (e.g., line bisection, cancellation, figure copying, etc.) (Farné, Rossetti, Toniolo, & Ladavas, 2002; Pisella, Rode, Farné, Boisson, & Rossetti, 2002; Pisella et al., 2006; Rossetti et al., 1998; Striemer & Danckert, 2010a, 2010b).

Subsequent studies have demonstrated that PA can reduce a variety of different neglect symptoms such as the rightward attentional bias, (Berberovic, Pisella, Morris, & Mattingley, 2004; Striemer & Danckert, 2007), the disengage deficit (Nijboer, McIntosh, Nys, Dijkerman, & Milner, 2008; Schindler et al., 2009; Striemer & Danckert, 2007), tactile extinction (Maravita et al., 2003), oculomotor biases (Serino, Angeli, Frassinetti, & Ladavas, 2006), and visual imagery (Rode, Rossetti, & Boisson, 2001). Interestingly, previous work by Striemer and Danckert (Striemer & Danckert, 2010a, 2010b) has suggested that PA may primarily reduce symptoms of neglect by influencing regions in the dorsal visual stream that are directly affected by PA (Danckert, Ferber, & Goodale, 2008; Luaute et al., 2006; Luaute et al., 2009; Saj, Cojan, Vocat, Luaute, & Vuilleumier, 2013; Shiraishi, Yamakawa, Itou, Muraki, & Asada, 2008; Striemer et al., 2008) and are known to play important roles in controlling motor responses such as reaching and eye movements (for a review see Milner & Goodale, 2006), as well as attention (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). In contrast, PA may have little effect on tasks which measure perception in the absence of an overt motor response (Dijkerman et al., 2003; Ferber, Danckert, Joanisse, Goltz, & Goodale, 2003; Striemer & Danckert, 2010a), or on non-spatially lateralized deficits such as spatial working memory (Striemer, Ferber, & Danckert, 2013), in patients with spatial neglect.

While rightward PA has been shown to reduce some symptoms of neglect, leftward PA has also been used to induce “neglect-like” patterns of behaviour in healthy individuals (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel, 2006; Michel, Pisella, et al., 2003). Specifically, when healthy individuals reach to targets while wearing leftward shifting prisms they initially miss far to the left. However, after a few reaches participants adjust their movements *rightward* to compensate for the leftward visual shift. Following adaptation if you ask participants to close their eyes and point straight-ahead they point far to the right, similar to patients with neglect *prior* to PA. In addition, leftward PA can also induce rightward shifts in manual line bisection (LB), as well as the landmark task (LM; i.e., a perceptual equivalent of line bisection) (Colent et al., 2000; Herlihey, Black, & Ferber, 2012; Michel, Pisella, et al., 2003; Schintu et al., 2014; Striemer & Danckert, 2010a). Furthermore, leftward PA has also been shown to influence covert visual attention (Striemer, Sablatnig, & Danckert, 2006), posture and balance (Michel, Rossetti, Rode, & Tilikete, 2003), tactile exploration (Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004), and attention to global and local features of a stimulus (Bultitude & Woods, 2010) in healthy adults.

Although PA can reduce symptoms of neglect in patients with right brain damage, and can induce “neglect-like” symptoms in healthy adults, the mechanisms underlying these effects remain unclear. One important question that remains to be directly addressed is whether the magnitude of the visual shift induced by prisms is in any way related to the magnitude of the effects of PA on attention and spatial biases. Specifically, during leftward prism adaptation, if the participant reaches to a target for the first time while wearing 10° leftward shifting prisms they will miss far to the left which generates an “error signal.” This error signal is based on a forward model that compares the mismatch between the sensory consequences of what the participant intended to do (i.e., reach to the target), versus what actually happened (i.e., missed far to the left) (for a review see Desmurget & Grafton, 2000). However, on subsequent trials the participant learns to compensate for this leftward visual shift by adjusting their movements rightward. This "recalibration" based on the error signal is thought to be one of the fundamental mechanisms underlying PA (Redding, Rossetti, & Wallace, 2005; Redding & Wallace, 2006). In addition, if participants adapt to a larger 20° leftward shift then they will initially miss *even further* to the left compared to when they are only exposed to a smaller (e.g., 10°) shift. The increased leftward shift will therefore result in a larger error signal (i.e., a larger mismatch between the forward model and the outcome of the movement). Given that a larger magnitude of leftward prism shift will generate a larger error signal, it will also necessitate an even greater rightward adjustment to compensate for this larger leftward shift. This greater rightward adjustment in reaching to compensate for the larger (20°) leftward should (theoretically) lead to an increased rightward aftereffect as measured by tasks such as subjective straight-ahead pointing. Importantly, it is not yet clear whether an increased error signal and subsequent aftereffect induced by a larger prism shift would have any significant influence on the effects of PA on tasks that measure attention and spatial biases. That is, while a number of previous studies have employed different magnitudes of shift *between studies* with many studies in patients using the standard 10° rightward shift first used by Rossetti and colleagues (1998) and many studies in healthy individuals using a 15° leftward shift as first used by Colent and colleagues (2000); very few studies have directly examined the effects of different magnitudes of prism shift on the same tasks *within the same study.*

Therefore, the purpose of the current study was to examine the effects of two different magnitudes of prism shift (8.5° vs. 17°) in healthy adults on measures of subjective straight-ahead, as well as tests of attention that are sensitive to the aftereffects of PA, manual LB, and the LM task (Colent et al., 2000; Michel, Pisella, et al., 2003; Striemer & Danckert, 2010a).

Previous work by Striemer and Danckert (Striemer & Danckert, 2010a, 2010b) has argued that PA may have a larger influence on tasks that require a motor response with the eyes or the adapted hand, as the brain structures controlling these effectors are directly influenced by PA (for a review see Striemer & Danckert, 2010b). Specifically, in a previous study (Striemer & Danckert, 2010a) we demonstrated that rightward PA significantly reduced the rightward bias in manual LB in patients with neglect; however, it had no influence on the LM task, a perceptual equivalent of the manual bisection task. If the aftereffects of prisms on attention and spatial biases are directly tied to the motor effectors influenced by prisms, then a larger magnitude of prism shift may have a differential influence on measures of attention that require a motor response with the adapted hand (i.e., LB), compared to a perceptual task with no manual component (i.e., the LM task). Therefore, in the current study we had two primary questions of interest: 1) will larger magnitudes of prism shift result in larger aftereffects (as measured by subjective straight-ahead pointing)? And 2) will larger magnitudes of PA have a differential effect on tasks that require a motor response with the adapted hand (i.e., manual LB) vs. a perceptual judgment (i.e., the LM task)?

Methods:

Participants

We recruited 47 right-handed undergraduate students (17 males; mean age = 21, SD= 3 years, range 18 to 33 years) from the MacEwan University student psychology participant pool and randomly assigned them to either an 8.5° (n=22) or a 17° (n=25) leftward shifting prisms group.

All participants were awarded course credit for participating. The experimental protocol was approved by the MacEwan University Research Ethics Board.

Procedure

During the testing session participants were seated with their head in a chin rest in front of table with a 32” horizontally mounted touch screen (ELO Touchsystems Inc.). The prism adaptation procedure and straight-ahead pointing tasks were carried out using the touch screen. During the LB and LM tasks the researcher covered the surface of the touchscreen with piece of thick black cardboard. This allowed participants to complete the LB and LM tasks without moving from the chinrest. Each of these tasks are described below.

At the beginning of the experiment all participants completed two blocks of LB and the LM task to establish a reliable pre-prisms baseline measure. Having two baseline measurements for each task allowed us to examine how reliable bisection and LM performance was prior to prism adaptation. Following the LB and LM tasks each participant completed the pre-prisms straight-ahead pointing task to get a baseline measure of subjective straight-ahead. Once baseline measures had been taken, participants were adapted to either 8.5° (n=22) or 17° (n=25) leftward shifting prisms (Bernell Products; see below for task description). These specific magnitudes of shift were chosen because 17° (30 diopter) was the largest magnitude available to us, and 8.5° (15 diopter) was exactly half of this magnitude. Following adaptation participants completed the post-prisms straight-ahead pointing task to measure the existence of any aftereffects. Following this participants completed the post-prisms LM and LB tasks. Note that the LM task was *always completed before the LB task* following prism adaptation as previous studies in healthy individuals have indicated that participants de-adapt from prisms if they perform the manual bisection task prior to the LM task (Striemer & Danckert, 2010a). At the end of the experiment participants completed the final straight-ahead pointing task to determine whether they remained adapted to prisms throughout the experiment.

Experimental tasks

Line bisection (LB) task: The LB task was completed on paper with a pen. Single horizontal black lines 20cm in length (2mm thickness) were presented individually on sheets of 8.5” x 11” paper aligned to participants’ midline. Participants were simply asked to mark with a single straight line, where they believed the center of the line was. There were 10 trials for each of the three blocks (two pre-prisms, one post prisms). To analyze the data we measured how far from center, in millimeters (mm), the participants made their bisection points. Bisections made to the left of center were recorded as negative values, and bisections made right of center were recorded as positive values. The average deviation from center was then calculated for each participant for each block of LB (pre 1, pre 2, post). In LB tasks healthy right handed participants typically bisect lines slightly to the left of midline (Jewell & McCourt, 2000). This is phenomenon, known as “pseudoneglect,” is thought to reflect the fact that the right hemisphere is dominant for attention and so it perceptually exaggerates the length of the left end of the line, thereby biasing the bisection mark to the left of midline (Jewell & McCourt, 2000; Milner, Brechmann, & Pagliarini, 1992).

Landmark (LM) task: During the LM task participants were asked to examine pre-bisected lines to determine if the bisection point was closer to the left or right side of the line (Milner et al., 1992; Striemer & Danckert, 2010a). On a single sheet of paper a horizontal black line 20 cm in length was bisected by a thin (1mm thick) black line on a white background. Sixteen lines were presented in total; 10 of the lines had the bisection point exactly at center. However, participants were unaware of this and were forced to choose either “closer to the left” or “closer to the right” for their response. The 6 remaining trials had lines that were bisected 1, 3, or 5 mm to left or right of center. These trials were included to ensure that participants were paying attention to the task and to ensure that they would not notice that all of the bisection markers were in exactly the same place on each line. Each block consisted of 16 trials (10 at center) presented in a pseudo-random order, for a total of 48 trials (32 before prisms). To analyze the data from the LM we calculated the percentage of trials in which participants decided the bisection point was “closer to the right” side of the line on the 10 trials where the bisection marker was actually at true center (Harvey, Milner, & Roberts, 1995) for each block of the LM (pre 1, pre 2, post). When the bisection marker is placed directly in the center of the line, healthy adults typically judge the marker as being “closer to the right” end of the line because the right hemisphere dominance for attentional exaggerates the length of the left end of the line (Jewell & McCourt, 2000; Milner et al., 1992).

Prism adaptation procedure: During the prism adaptation task participants pointed to targets presented on the touch screen that were located 10cm to the left and right of their body midline while wearing prisms that shifted vision either 8.5° (n=22) or 17° (n=25) to the left. During a single trial the participant pressed and held down a mouse button located just in front of the touch screen with their right index finger. Then a target appeared on the screen 10cm to the left or right of center, and the participant had to release the mouse button and point to the target as quickly and accurately as possible. The participant then returned their finger back to the mouse button and made their next pointing movement when another target appeared. During the adaptation procedure the participant's hand was only partially visible at the start of the reach, but became visible as soon as they initiated their reach towards the target (i.e. concurrent feedback). There were pointing 200 trials in total (presented in a random sequence) which took around 7 - 10 minutes to complete depending on how much time participants waited between pointing movements.

Straight-ahead pointing task: During this task participants were asked to close their eyes and reach out straight-ahead of their body midline and touch the surface of the touch screen. This was repeated five times to get a reliable measure of subjective straight-ahead. This task was performed once prior to PA (pre), once immediately following adaptation (post), and once more at the end of the experiment (final). To analyze the straight-ahead pointing data we measured (in centimeters) how far the endpoint of the participant's pointing movement was from true center. Touches made to the left of center were recorded as negative values, and touches made right of center were recorded as positive values. The endpoints were then averaged across the five pointing trials within each block (i.e., pre, post, and final) in order to examine whether or not any adaptation effects had occurred.

Statistical analysis

To compare the effects of prism adaptation on straight-ahead pointing we used an ANOVA with group (8.5° vs. 17° prisms) as a between-subject factor and time (pre, post, final) as a within subject factor. To examine the effects of PA on the LB and LM tasks we used an ANOVA with group (8.5° vs. 17° prisms) as a between-subject factor and time (pre vs. post) as a within-subject factor. Post-hoc tests were carried out when necessary using t-tests with a Bonferroni correction.

Results:

Prism adaptation

In order to assess whether participants adapted to prisms, and whether or not there were any significant differences in the magnitude of the after effects observed between the 8.5° and 17° leftward shifting prisms groups, we used a mixed model ANOVA with group (8.5° vs. 17°) as a between-subject factor and time (pre vs. post vs. final) as a within-subject factor. This analysis revealed significant main effects of group (F(1,45)=5.37, *p*=.025, η_p^2=.11) and time (F(2,90)=37.97, *p*<.001, η_p^2=.46). Specifically, participants pointed further rightward in the 17° group (6.16cm) compared to the 8.5° (3.68cm) group. In addition, participants were adapted further rightward in the post (6.42cm; t(46)=6.80, *p*<.001) and final (6.13cm; t(46)=7.65, *p*<.001) pointing sessions compared to the pre PA session (2.45cm); however, there was no significant difference between the post (6.43cm) and final (6.13cm) pointing sessions (t(46)=0.58, *p*=.56). Finally, there was also a significant group x time interaction (F(2,90)=6.39, *p*=.003; Figure 1, η_p^2=.12). To examine the source of this interaction we analyzed simple main effects for the 8.5° and 17° prisms groups at each level of time (i.e., pre, post, and final). These contrasts indicated that there were no significant differences between the two groups at baseline (8.5°=2.2cm vs. 17°=2.67cm; t(45)=.45, *p*=.68). Post PA there was a trend towards a larger rightward shift following adaptation to 17° (7.93cm) compared to 8.5° (4.70cm) prisms (t(45)=2.31, *p*=.026, *p*=.078 corrected). At the final pointing session at the end of the experiment there was a larger rightward shift in straight-ahead pointing for the 17° (7.89cm) compared to the 8.5° prisms group (4.13cm; t(45)=3.38, *p*=.006, corrected).

--Insert Figure 1 here---

Baseline bisection and landmark performance

Prior to examining the LB and LM data for any effects of PA we first evaluated whether there were any differences in performance in these two tasks between the two baseline conditions in each group. Note that for one participant, due to an experimenter error, we only had data from one baseline test in the LB task. For this participant we therefore used this single measurement as their baseline performance. In order to examine whether performance differed across the two baselines we averaged LB and LM performance separately across the 8.5° and 17° leftward shifting prisms groups. We then compared performance for baselines 1 (B1) and 2 (B2) using paired samples t-tests. This analysis revealed that there were no significant differences in performance between B1 and B2 for either the LB (B1=0.37mm; B2=0.38mm; t(45)=.025=, *p*=.98) or the LM tasks (B1=55%, B2=55%; t(46)=.19, *p*=.85). This is consistent with recent work indicating that LB and LM task performance is stable over time within participants (Learmonth, Gallagher, Gibson, Thut, & Harvey, 2015). Given that the two baselines were equivalent for each task we collapsed them into a single baseline condition to compare with the post PA condition.

Line bisection pre vs. post prisms

All data from the LB and LM tasks pre and post PA for the 8.5° and 17° leftward shifting prisms groups are presented in Supplementary Tables 1 and 2. To examine LB performance pre and post PA we conducted a mixed-model ANOVA with group (8.5° vs. 17°) as the between-subject factor and time (pre vs. post) as a within-subject factor. This analysis revealed no main effects (all *p*'s >.15), but a significant group x time interaction ($F(1,45)=6.90$, $p=.012$, $\eta_p^2=.13$; Figure 2a). To examine this interaction we compared pre and post LB performance separately for the 8.5° and 17° groups. These contrasts revealed that leftward PA resulted in a significant rightward shift in LB in the 17° prisms group (pre= -0.31mm vs. post=0.84mm, $t(24)=3.06$, $p=.01$, corrected) but not the 8.5° prisms group (pre=0.99mm vs. post=0.67mm; ($t(21)=.770$, $p=.90$, corrected).

Inspection of Figure 2a suggests that baseline performance in the LB task was slightly to the left of center for the 17° group (-.31mm), but slightly to the right of center for the 8.5° degree group (.99mm). However, a formal comparison of baseline performance between these two groups revealed no significant difference ($t(45)=1.57$, $p=.12$, uncorrected). One might argue, however, that this tendency towards baseline differences in performance between the two groups may have made it harder to demonstrate any further rightward shift in LB performance in the 8.5° group following leftward PA. To further address this potential issue we removed any participants from the two groups whose pre prisms LB performance was more than 2SDs above or below the group mean for that condition (see Supplementary Tables 1 and 2). Following the removal of outliers there were 15 participants remaining in the 8.5° group (i.e., 7 participants removed), and 21 participants remaining in the 17° group (i.e., 4 participants removed). The removal of these outliers brought the pre prisms LB performance of the 8.5° prisms group much closer to center (Figure 2b). However, even after removing these extreme scores, the same pattern of results emerged. That is, there was a significant rightward shift in LB following 17° (pre= -.49mm vs. post=.74mm; t(20)=2.84, *p*=.02, corrected) but not 8.5° (pre=.21mm vs. post=.06mm; t(14)=.27, *p*=.79) leftward shifting prisms (Figure 2b).

--Insert Figure 2 here--

Landmark task pre vs. post prisms

To examine LM performance pre and post PA we conducted a mixed-model ANOVA with group (8.5° vs. 17°) as the between-subject factor and time (pre vs. post) as a within-subject factor. This analysis revealed a significant main effect of time, (F(1,45)=5.90, *p*=.019, η_p^2=.12), such that the percentage of "closer to the right" responses was significantly decreased post (48%, SD=19) compared to pre PA (55%, SD=19). However, there was no main effect of group, and no group x time interaction (all *p*'s >.38). [1]

Correlations between changes in task performance and changes in straight-ahead pointing

One of our primary hypotheses was that larger magnitudes of prism shift would have greater effects on tasks that required a manual response with the adapted hand (i.e., LB) compared to

[1] Note that in addition to testing 8.5° and 17° leftward shifting prisms groups, we also tested a 17° rightward shifting prisms group (n=22) as a control. Although we were able to demonstrate a significant leftward after effect in straight-ahead pointing in the rightward shifting prisms group (pre= 1.09 vs. post= -2.58, *p*=.016, corrected), there were no significant changes in either LB (pre= -.74 vs. post= -1.03; F(1,21)=.824, *p*=.37) or the LM task (pre=55% vs. post=53%; F(1,21)=.28, *p*=.60) following rightward prism adaptation. This result is similar to previous studies that have failed to find significant effects of rightward shifting prisms on tests of attention and perceptual biases in healthy adults (e.g. Colent et al., 2000).

tasks that required a perceptual judgment (i.e., the LM task). This hypothesis was supported by the fact that 17° leftward shifting prisms caused a significant rightward shift in LB performance, whereas 8.5° prisms had no effect. However, both 8.5° and 17° leftward shifting prisms resulted in reductions in the leftward bias in the LM task. To further investigate the link between PA magnitude and changes in LB and LM performance we conducted a correlation analysis that examined the relationship between the aftereffects of prisms (as measured by straight-ahead pointing) and performance on the LB and LM tasks. To do this we computed difference scores between the pre and final straight-ahead pointing sessions (where there was a significant difference between the groups in the straight-ahead pointing analysis) and then correlated this measure with difference scores for pre vs. post LB and pre vs. post LM performance. This analysis revealed a significant positive correlation between changes in straight-ahead pointing (pre vs. final; $r(47)=.49$, $p=.001$) and changes in the LB performance pre vs. post PA (Figure 3a). However, there was no significant correlation between changes in straight-ahead pointing (pre vs. final) with changes in LM task performance pre vs. post PA ($r(47)= -.16$, $p=.29$; Figure 3b).

--Insert Figure 3 here--

Discussion:

In the current study we examined whether the magnitude of prism shift (i.e., 8.5° vs. 17°) has any influence on the magnitude of prism aftereffects induced on tests of attentional and spatial biases. In order to investigate whether the magnitude of prism shift has any influence on aftereffects, and tests of attentional biases, we had groups of healthy adults complete a manual LB task and a LM task before and after adapting to either 8.5° (n=22) or 17° (n=25) leftward shifting prisms.

Our results indicated that, as predicted, larger magnitudes of prism shift led to larger aftereffects as measured by straight-ahead pointing. Specifically, there was no difference in straight-ahead pointing between the 8.5° and 17° groups at baseline; however, there was a trend towards a larger rightward shift in straight-ahead pointing for the 17° group following PA, and this difference was significant by the “late” pointing session at the end of the experiment (Figure 1). The results from the LB task revealed a significant time x group interaction. Specifically, there was a significant rightward shift in LB following PA for the 17° group, but not the 8.5° group (Figure 2). The results from the LM task revealed a significant reduction in “closer to the right” responses following PA; however, there was no interaction with group, and no time x group interaction. Thus, prism magnitude did not differentially influence performance on the LM task pre vs. post PA. Finally, a correlation analysis (Figure 3) examined whether the magnitude of the PA aftereffect (as indexed by changes in straight-ahead pointing) was correlated with changes in LB and LM task performance pre vs. post prisms. This analysis revealed a significant positive correlation between changes in straight-ahead pointing (pre vs. final) with changes in LB performance pre vs. post PA (Figure 3a). However, we observed no significant correlation between changes in straight-ahead pointing and changes in LM task performance pre vs. post PA (Figure 3b).

The results from the current study differ from those of two recent studies examining the effects of prism magnitude on behavior in some important respects. First, a recent study by Facchin et al. (2013) examined the effects of different magnitudes of rightward prism shift of 3°, 6°, and 11° (5, 10, and 20 diopters respectively) on LB performance in a group of 5 patients with neglect. The results of their study demonstrated that there were no significant changes in straight-ahead pointing or LB performance following PA. However, there were trends towards reductions in the rightward bias in LB regardless of the PA magnitude used. In contrast, in the current study we observed a significant rightward shift in straight-ahead pointing following leftward PA in both the 8.5° and 17° prisms groups. In addition, the 17° group also demonstrated a significant rightward shift in LB performance.

One obvious difference between the current study and that of Facchin and colleagues (2013) is that they examined patients with neglect whereas we examined healthy individuals. As such, their failure to find changes in straight-ahead pointing as a function of prism magnitude in their patient group may reflect the small size of the group (n=5), or the inherent heterogeneity of patients with neglect. Another important difference between the two studies was that they used 11° as their largest magnitude of prism shift with two smaller prism shifts (3° and 6°) as comparisons. Perhaps a larger magnitude of prism shift would have led to a greater leftward shift in LB behaviour in their patient group.

Another recent study by Michel and Cruz (2015) also examined the influence of different magnitudes of leftward prism shift (8°, 10°, 15°) on LB and LM performance in healthy adults. Their results demonstrated, similar to the current study, that significant differences in straight-ahead pointing emerged only at the end of the experiment (although there was a trend towards a larger shift immediately post prisms in the current study). The results from their LB task indicated that only the 10° and 15° groups experienced a significant rightward shift in bisection performance. This is consistent with the current study in that we only observed a rightward shift in bisection in our 17° group, but not our 8.5° group. Although we did not include a 10° leftward shifting prisms group in the current study (i.e., the same magnitude of shift used in most studies of patients with neglect), we would predict the same results that were obtained in the current study. Namely, that a larger magnitude of prism shift (i.e., 17°) should lead to a larger change in

LB performance pre vs. post PA than a smaller shift (i.e., 10°), and that changes in LB pre vs. post PA should continue to be correlated with changes in straight-ahead pointing pre vs. post PA.

One important difference between our findings and those of Michel and Cruz (2015) is that in their results for the LM task, only the 15° group demonstrated a significant change in LM performance post-adaptation. In contrast, we observed a significant change in LM performance in both the 8.5° and 17° groups. It should be pointed out that different methods were used to measure changes in performance in the LM task pre vs post prisms in the two studies. Specifically, Michel and Cruz (2015) used lines bisected at true center, as well as varying distances (2-8mm) to the left and right of center in order to estimate the point of subjective equality, and thus the perceived midpoint. In contrast, we examined the percentage of trials in which the participant responded that the bisection marker was "closer to the right" end of the line on trials where the bisection marker was exactly in the middle. Although one might argue that our method is less sensitive, this appears not to be the case, as we were able to detect significant changes in both the 8.5° and 17° groups using these methods in the current study. One possible explanation for these differences is the small sample size (n=8 in each group) used by Michel and Cruz (2015) compared to the larger samples used in the current study (n>22 in each group). That is, the larger sample sizes used in the current study would have increased our power to detect subtle changes in performance following a smaller (i.e., 8.5°) magnitude of PA. In addition, healthy adults might be quite good at detecting subtle changes in the position of the bisection marker (e.g., even 1-2mm) making it harder to uncover a perceptual bias on this version of the task. However, when a majority of the bisection markers are in the middle (unbeknownst to the participant), and there is no correct answer, it may be easier to uncover a perceptual bias as was observed in the current study.

One final difference between our results and those of Michel and Cruz (2015) is that they observed a significant correlation between PA aftereffects (i.e., changes in straight-ahead pointing pre vs. post) and changes in LM task pre vs. post PA; however, they did not observe any correlation between the PA after effect and changes in the LB task. This finding is at odds with the results of the current study in that we observed the exact opposite pattern of results. Specifically, we only observed a significant correlation between changes in straight-ahead pointing (pre vs. final) and changes in LB pre vs. post PA. In contrast, we observed *no correlation whatsoever* with changes in the LM task pre vs. post PA. Again, one could argue that the differences in the methods used to measure LM task performance between the two studies (see above) might have prevented us from observing any correlation between PA aftereffects and changes in the LM task pre vs. post PA. However, this seems unlikely as we were clearly able to detect changes in LM performance pre vs. post in both the 8.5° and 17° groups. Therefore, the current results suggest that, while prisms can influence both LB and LM performance in healthy adults, the effects of PA on these two tasks arise via distinctly different (and independent) mechanisms.

The fact that the magnitude of the PA aftereffect was related to tasks that were completed with the same hand that adapted to prisms (i.e., LB), but had no differential effect on a perceptually equivalent task (i.e., LM) is generally consistent with previous work in patients with neglect. Specifically, previous research has demonstrated that PA can significantly reduce symptoms of neglect on tasks that require a response with an effector that is directly influenced by the PA procedure (i.e., the eyes or the hand), but have little to no effects on purely perceptual tasks (Dijkerman et al., 2003; Ferber et al., 2003; Striemer & Danckert, 2010a, 2010b). It should be noted that while previous studies have shown differential effects of PA on LB and LM task performance in patients with neglect, in the current study, we observed significant changes in LM performance following PA in healthy adults (see also Colent et al., 2000; Michel & Cruz, 2015; Michel, Pisella, et al., 2003). This suggests that it is *possible* for PA to influence perceptual measures of spatial biases; however, this rarely seems to happen in patients with neglect. As we have argued previously, this is likely because the PA has differential effects on the dorsal and ventral streams of visual processing (Striemer & Danckert, 2010a, 2010b), and the critical lesion site in neglect, the temporo-parietal junction (TPJ), is a region that may be important for integrating information between the two streams (Husain & Nachev, 2007; Milner & Goodale, 2006). Thus, it is possible that damage to the TPJ could result in dissociable effects on tasks that differentially recruit the two streams (i.e., a larger effect of PA on tasks that engage the dorsal stream). This may be why PA has been shown to reduce the rightward bias in LB (e.g.,Farné et al., 2002; Pisella et al., 2002; Rossetti et al., 1998; Striemer & Danckert, 2010a) in patients with neglect, but has never (at least to our knowledge) been shown to alter performance on the LM task. In contrast, in healthy adults where the TPJ is intact it is possible for prisms to influence tasks that require both manual and perceptual responses, but the effects of PA on these two tasks arise via distinctly different (i.e., independent) mechanisms.

It should be noted that the size of the rightward shift in LB produced by leftward shifting prisms was somewhat smaller in the current study (1.1mm in the 17° group) compared to some previous studies. However, the rightward shift in LB induced by leftward shifting prisms varies considerably from study to study from as large as 5.75mm (Michel & Cruz, 2015) to as small as ~2mm (Michel, Pisella, et al., 2003) even when the same procedures are used by the same investigators. Thus, just as LB performance varies considerably from subject to subject in healthy adults (Jewell & McCourt, 2000), so to do the effects of prisms on LB performance. The most important thing to emphasize is that even though the rightward shift in LB we observed was small, it was statistically reliable. Furthermore, changes in LB behaviour pre vs. post-prisms were also significantly correlated with changes in straight-ahead pointing pre vs. post-prisms.

The results of the current study have important implications for understanding the mechanisms by which prisms exert their influence on attention and spatial biases. First, we have demonstrated that larger prism shifts lead to larger aftereffects as measured by straight-ahead pointing. This knowledge could prove beneficial for using PA to treat neglect. For example, if a patient with neglect has a larger rightward deviation in their egocentric reference frame, then a larger magnitude of prism shift may be more effective in reducing their symptoms than a smaller one. Again, although the effects we observed in in the present study were small (1.1mm), this would likely translate into a much bigger effect in patients with neglect as it is well known that the effects of PA in patients with neglect are substantially larger than those in healthy adults (Pisella et al., 2006; Redding & Wallace, 2006). For example, in one of our previous studies we observed a 2.8mm rightward shift in LB in healthy older adults following leftward PA, whereas we observed a 26mm leftward shift in LB following rightward PA (Striemer & Danckert, 2010a). In addition to reducing the rightward bias in LB in patients with neglect, one might also predict that a larger magnitude of prism shift should result in a greater reduction in neglect symptoms in tasks that involve motor responses such as a manual response with the adapted hand, or the use of eye or arm movements towards the contralesional field. This will be an important topic for future studies.

Although we failed to find an effect of prisms on LB in our 8.5° group, an alternative LB task, such as presenting the lines to the left or right of body midline (i.e., the line location effect), might be able to reveal more subtle effects of prisms on LB performance (Jewell & McCourt, 2000; Michel, Pisella, et al., 2003). Future research could also examine the extent to which different magnitudes of prism shift influence performance on a variety of tasks that are known to be sensitive to the effects of PA such as covert attention (Striemer et al., 2006), or the greyscales task (A. M. Loftus, Vijayakumar, & Nicholls, 2009). It would also be of interest to examine whether the adaptation aftereffects from a larger magnitude of prism shift (e.g., 17°) are *longer lasting* than the aftereffects from a smaller prism shift (e.g., 8.5°). According to data from the current study, there were no obvious differences in de-adaptation rates when comparing post and final straight-ahead pointing in the 8.5° and 17 groups° (see Figure 1). However, differences in de-adaptation rates may emerge if straight-ahead pointing were tested over a longer timescale. Furthermore, it would also be interesting to examine whether different methods of PA, such as concurrent vs. terminal feedback, are more (or less) effective in elucidating the influence of different magnitudes of PA on attentional and spatial biases.

Finally, future studies could also examine the extent to which different magnitudes of prism shift influence different measures of PA aftereffects such as open-loop pointing or visual straight ahead as this would enable a better understanding of the reference frames are altered by different magnitudes of shift. Recent data from Facchin and colleagues suggests that open-loop pointing may be a more sensitive measure of the PA aftereffect induced by different magnitudes of shift in both patients with neglect (Facchin, Beschin, et al., 2013), and healthy adults (Facchin, Toraldo, & Daini, 2011). However, the current study, as well as that of Michel and Cruz (2015), suggest that straight-ahead pointing is a sensitive measure of the PA aftereffect as it relates to prism magnitude, at least, in healthy adults. In addition, the results from the present study demonstrate that changes in straight-ahead pointing pre vs. post PA are correlated with changes in LB performance pre vs. post PA.

Conclusion:

In summary, we have demonstrated that larger magnitudes of prism shift have a greater effect on tasks that require manual responses (i.e., LB) compared to perceptual judgments (i.e., the LM task). Furthermore, we have also demonstrated that changes in straight-ahead pointing following prism adaptation are *positively correlated* with changes in performance on tasks that require manual (i.e., LB), but not perceptual judgments (i.e., the LM task). Taken together, our data add to the growing body of evidence which suggests that prism adaptation has differential (and largely independent) effects on measures of attentional biases that require manual vs. perceptual responses.

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Figure 1. Depicts the magnitude of rightward shift in straight-ahead pointing (in cm) as a function of time (pre, post, final) and group (8.5° vs. 17°). Error bars represent the standard error.* indicates that the comparison is significant without a Bonferroni correction.

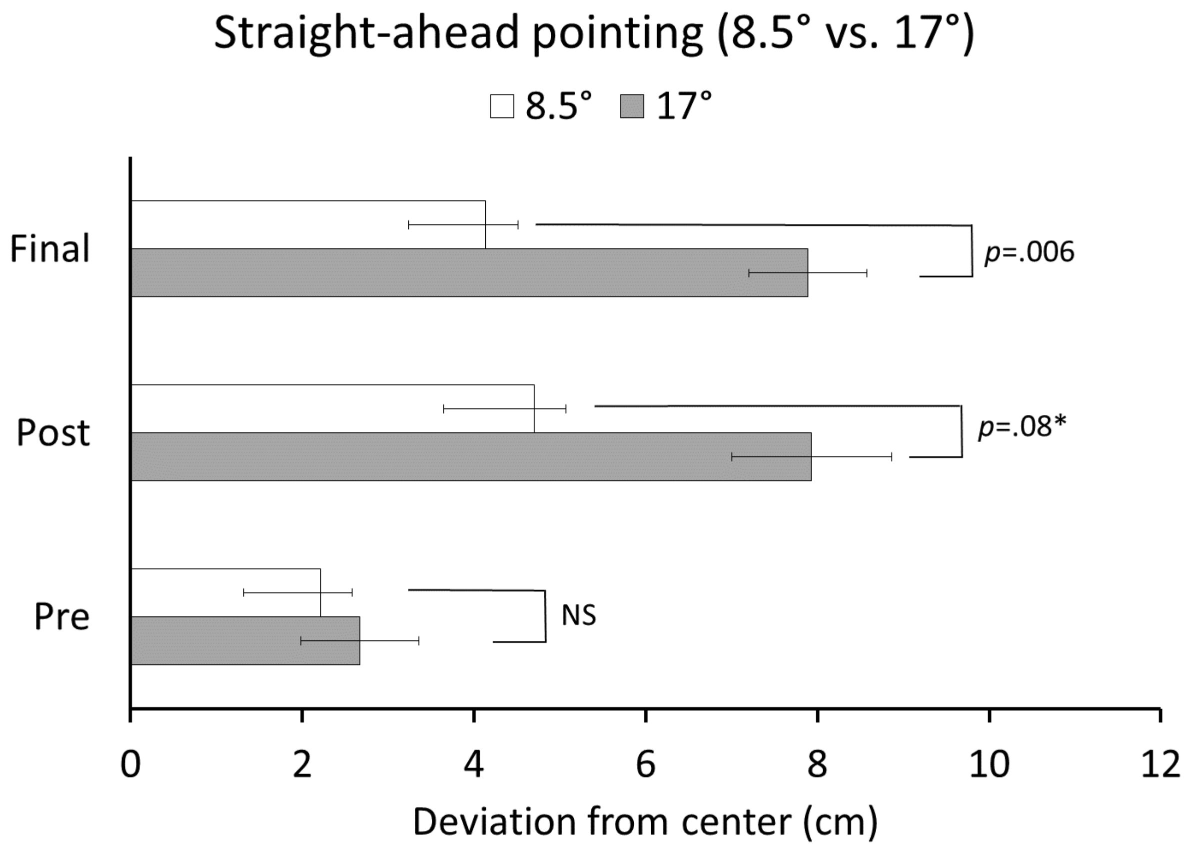

Straight-ahead pointing (8.5° vs. 17°)
8.5°
17°
Final
Post
Pre
p=.006
p=.08*
NS
0
2
4
6
8
10
12
Deviation from center (cm)

Figure 2. A) Depicts the results from the line bisection (LB) task (in mm) as a function of time (pre vs. post prisms) and group (8.5° vs. 17°). B) Depicts the results from the line bisection task with outliers removed from each group as a function of time (pre vs. post) and group (8.5°, n=15 vs. 17°, n=21). For both graphs, negative values are left of center whereas positive values are right of center. Error bars represent the within-subject standard error (G. R. Loftus & Masson, 1994).

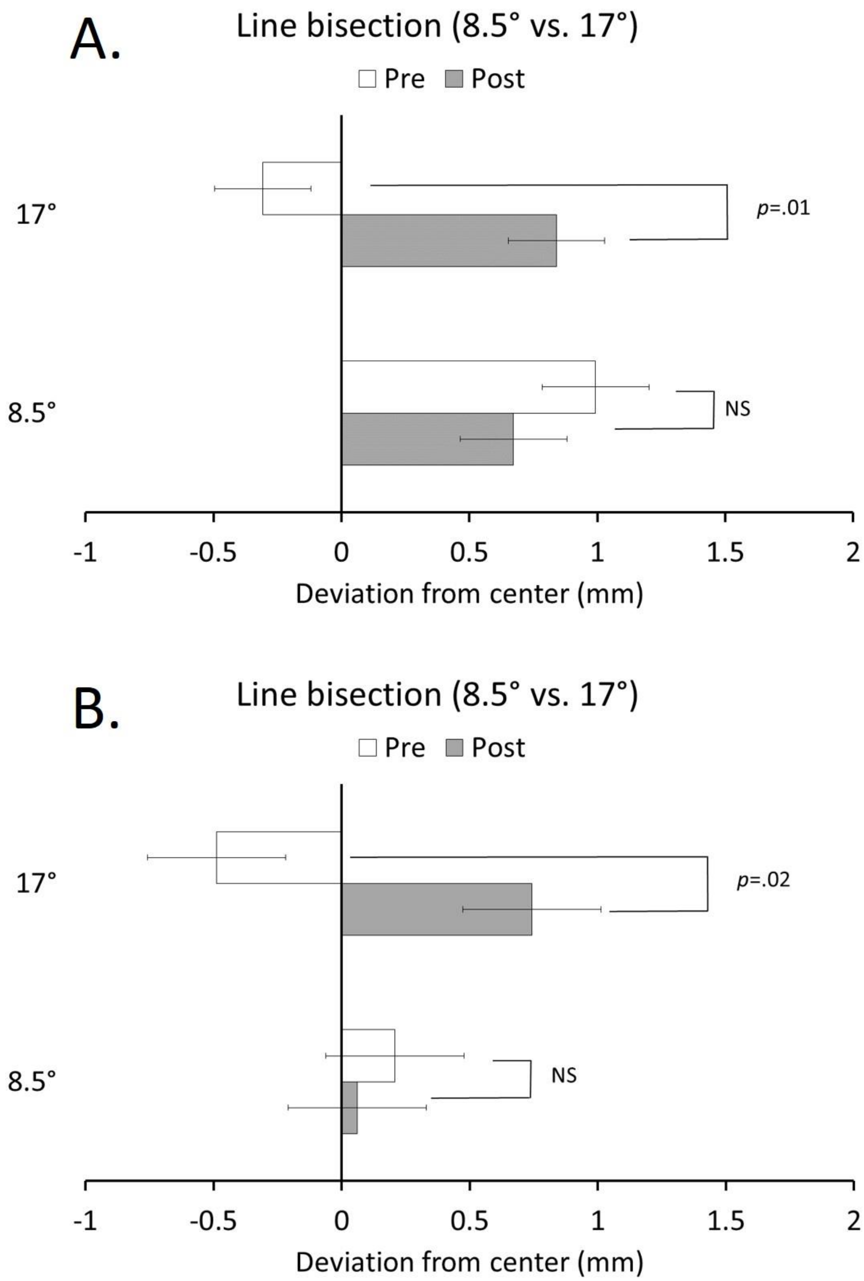
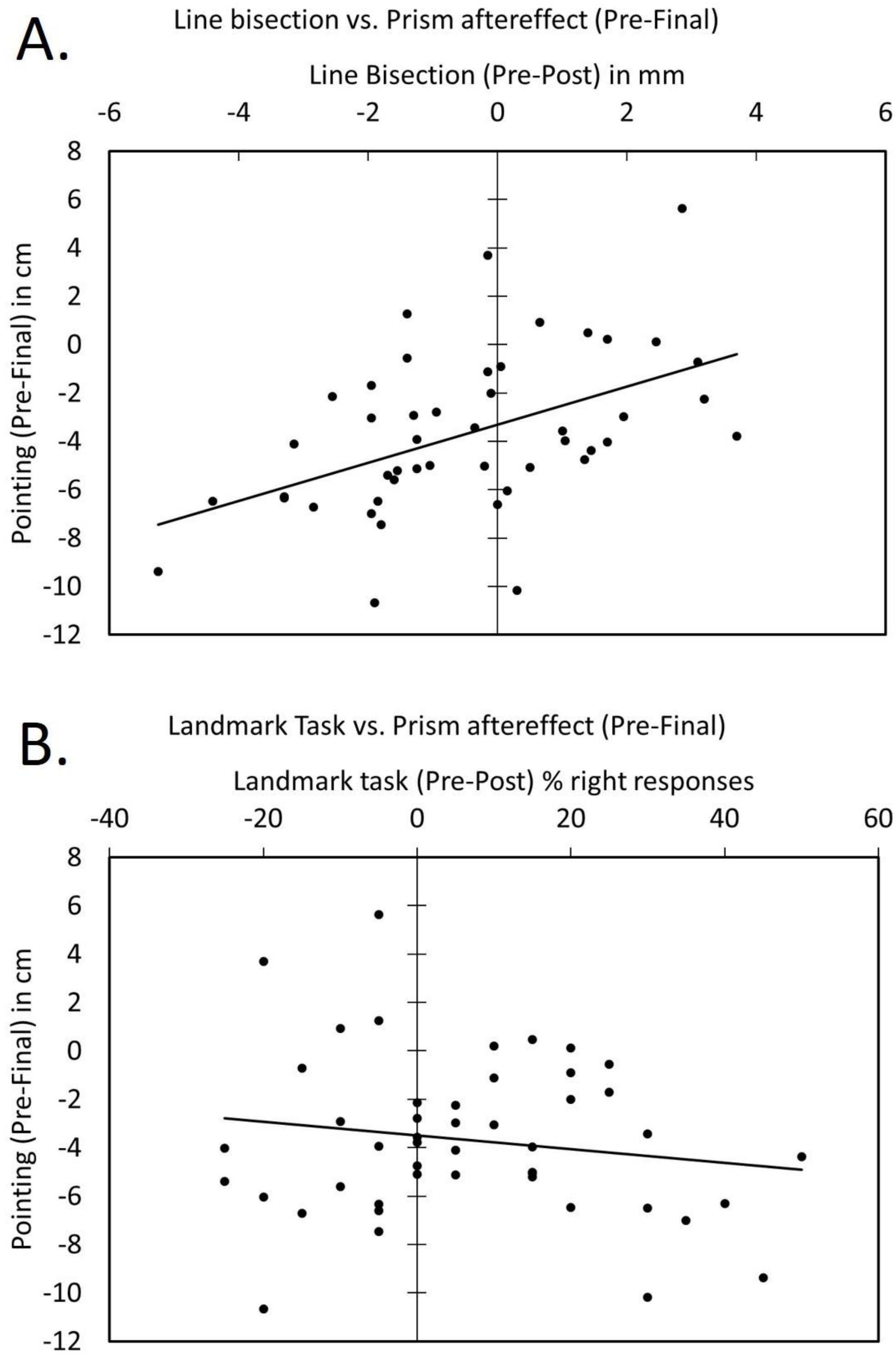


Figure 3. A) Depicts the correlation between changes in line bisection performance (pre-post) and prism aftereffect (pre-final). B) Depicts the correlation between changes in landmark task performance (pre-post) and prism aftereffect (pre-final).



Supplementary Table 1: Data from the line bisection and landmark tasks pre vs. post prism adaptation for the 8.5° leftward shifting prisms group. Line bisection data are reported as deviation from center in millimeters. Landmark data are reported as the percentage of “closer to the right” responses. * indicates a participant that was flagged as an outlier for the analysis depicted in Figure 2B in the primary manuscript.

Participant:	Group:	Line Bisection Pre:	Line Bisection Post:	Landmark Pre:	Landmark Post:
1	8.5°	2.65	1.60	45	30
2	8.5°	0.20	-3.50	50	50
*3	8.5°	6.15	3.30	45	50
6	8.5°	2.05	0.70	30	30
*8	8.5°	3.75	3.90	30	50
*13	8.5°	3.55	5.50	45	20
14	8.5°	-0.95	-2.40	90	40
16	8.5°	0.95	1.30	70	40
*17	8.5°	2.40	0.70	70	60
19	8.5°	-0.25	2.60	55	70
21	8.5°	2.50	-0.60	45	60
22	8.5°	1.20	-0.50	25	50
*23	8.5°	-4.20	-4.10	60	40
26	8.5°	1.30	-0.10	65	50
28	8.5°	0.55	3.10	60	60
*33	8.5°	2.85	2.80	60	40
36	8.5°	-5.05	-1.90	45	40
*40	8.5°	4.25	1.80	40	20
41	8.5°	-1.05	-1.20	40	60
43	8.5°	5.55	6.80	45	50
45	8.5°	-5.40	-4.00	75	80
46	8.5°	-1.15	-1.00	50	40
	Mean	**0.99**	**0.67**	**51.82**	**46.82**
	SD	**3.11**	**2.95**	**15.85**	**14.92**

Supplementary Table 2: Data from the line bisection and landmark tasks pre vs. post prism adaptation for the 17° leftward shifting prisms group. Line bisection data are reported as deviation from center in millimeters. Landmark data are reported as the percentage of “closer to the right” responses. * indicates a participant that was flagged as an outlier for the analysis depicted in Figure 2B in the primary manuscript.

Participant:	Group:	Line Bisection Pre:	Line Bisection Post:	Landmark Pre:	Landmark Post:
4	17°	-0.30	3.00	80	40
5	17°	-2.35	-0.50	100	80
7	17°	0.40	-2.80	75	70
9	17°	-3.80	0.60	60	30
10	17°	1.55	2.60	55	40
11	17°	0.35	1.90	75	60
*12	17°	6.10	5.60	20	20
*15	17°	3.70	5.30	30	40
*18	17°	-3.2	-3.40	65	50
20	17°	-2.40	-2.40	45	50
24	17°	-2.20	1.10	45	50
25	17°	-1.95	-0.70	95	90
27	17°	-3.75	-4.40	80	90
29	17°	-1.50	-0.20	40	50
30	17°	1.80	0.80	40	40
31	17°	2.00	3.80	65	70
32	17°	-2.70	-1.00	35	60
34	17°	0.25	5.50	65	20
35	17°	0.90	0.60	30	0
37	17°	-1.55	-0.60	80	80
38	17°	-0.60	1.30	40	60
*39	17°	-4.05	-2.10	75	40
42	17°	2.55	4.50	50	40
44	17°	1.45	-0.50	55	50
47	17°	1.60	3.00	45	20
	Mean	**-0.31**	**0.84**	**57.80**	**49.60**
	SD	**2.51**	**2.82**	**21.12**	**22.63**

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