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Accepted in: *Cortex* on January 25, 2019

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Abstract:
Prism adaptation is a time-honored tool for studying how the motor system adapts to sensory perturbations. Past research on the neural substrates of prism adaptation has implicated the posterior parietal cortex (PPC) and the cerebellum, under the assumption that these structures gain their visual input from the dominant retinogeniculate pathway to V1. Here we question whether this pathway is even required for visuomotor adaptation to occur. To investigate this, we examined prism adaptation in 'MC,' someone who is blind to static stimuli following bilateral lesions that encompass much of her occipital cortex and the caudal-most areas of ventrotemporal cortex. Remarkably, MC shows evidence of prism adaptation that is similar to healthy control participants. First, when pointing with either the left or the right hand, MC shows *spatial realignment*; the classical after-effect exhibited by most people when adapting to displacing prisms. Second, MC demonstrates *strategic recalibration* – a reduction in her pointing error over time – that is similar in magnitude to healthy controls. These findings suggest that the geniculostriate pathway is not necessary for visuomotor adaptation to take place. Alternatively, we suggest that an extrageniculostriate pathway which provides visual inputs to the cerebellum from area MT and the PPC via the dorsolateral pons plays a significant and appreciable role in the guidance of unconscious, automatic visuomotor adaptation.

Keywords: Prism adaptation, cerebellum, blindsight, posterior parietal cortex, visual pathways

Introduction:

For over 100 years, prism adaptation (PA) has been the model paradigm for studying how the sensorimotor system uses sensory and motor information to minimize movement error (Helmholtz & Southhall, 1924). In a standard PA task, participants wear glasses that shift their visual array in one direction or another and are asked to reach out to touch a visual target as swiftly and accurately as they can. Initially, participants misreach for the target in the direction of the shifted visual array. Yet, within a few trials the discrepancy between the target and finger endpoint is minimized. Thus, participants not only register the discrepancy between the target and their reach, they also incorporate this information into their subsequent movements to reduce the discrepancy on future trials.

Previous research suggests that adapting to prisms entails at least two distinct but interacting processes. The first process, *strategic recalibratio*n operates over the first few reaches, while the second process, *spatial realignment*, operates over a much larger number of iterations (for an authoritative review see Redding, Rossetti, & Wallace, 2005). Using visuomotor feedback from the first few trials, participants reduce errors "strategically" by voluntary compensating and pointing in the direction opposite the prism shift. For example, after several pointing trials while wearing rightward shifting prisms, participants "recalibrate" and successfully hit the target by adjusting their movements with *leftward* compensation (Redding et al., 2005). Critically, if the prisms are removed after these first few trials, no after-effects are observed. However, if participants continue to make numerous iterative reaches toward the target while wearing prisms, *spatial realignment* occurs. This refers to the finding that when prisms are removed, participants misreach in the direction opposite the prism shift (Redding et al., 2005). Of course, the after-effect dissipates as a new round of adaptation occurs in response to the new

stable environment (i.e., with the prisms removed); sometimes referred to as the *washout* phase. If the participant is allowed visual feedback during the washout phase, pointing will rapidly return to pre-prism baseline (Redding et al., 2005). However, if visual feedback is withheld, then participants can remain adapted for an extended period of time (e.g., Striemer & Borza, 2017). In summary, while *strategic recalibration* is thought to require voluntary participation, *spatial realignment* is thought to be a relatively automatic, via an involuntary process that remaps the spatial reference frames amongst eye and limb effectors (Redding et al., 2005).

The notion that PA can be used to realign spatial reference frames in the direction opposite the prism shift was a precursor for the development of PA to treat symptoms of spatial neglect (Rossetti et al., 1998) – a disorder in which patients are unable to attend to stimuli on the side opposite their lesion (for reviews see Danckert & Ferber, 2006; Husain & Rorden, 2003). A seminal paper by Rossetti and colleagues (Rossetti et al., 1998) – which is the focus of this special issue – demonstrated that it was possible to reduce symptoms of left spatial neglect by using rightward shifting prisms to realign the patients' egocentric reference frame leftward (i.e., toward their neglected field). Following this study there was tremendous interest in better understanding how PA reduced symptoms of neglect (for reviews see Newport & Schenk, 2012; Pisella, Rode, Farné, Tilikete, & Rossetti, 2006; Redding & Wallace, 2006; Rode, Klos, Courtois-Jacquin, Rossetti, & Pisella, 2006; Striemer & Danckert, 2010), and how PA might influence attention and perception in healthy adults (for reviews see Michel, 2006, 2015).

At the same time, there has been a renewed interest in the neural mechanisms underlying PA. One popular model of PA, based largely on lesion studies in humans and non-human primates, suggests that *strategic recalibration* is controlled by the posterior parietal cortex (PPC) in the dorsal visual stream, whereas *spatial realignment* is controlled by the cerebellum

(Newport, Brown, Husain, Mort, & Jackson, 2006; Newport & Jackson, 2006; Pisella et al., 2004; Redding et al., 2005). Specifically, patients with optic ataxia following PPC lesions that have difficulty with visually guided actions may show slowed *strategic recalibration*, yet they still demonstrate *spatial realignment* (Newport & Jackson, 2006; Pisella et al., 2004; Striemer et al., 2008) [1]. In contrast, lesions to the cerebellum may not impair *strategic recalibration* (e.g., Weiner, Hallett, & Funkenstein, 1983; Werner, Bock, Gizewski, Schoch, & Timmann, 2010), but disrupt spatial realignment (Baizer, Kralj-Hans, & Glickstein, 1999; Martin, Keating, Goodkin, Bastian, & Thach, 1996; Norris, Hathaway, Taylor, & Thach, 2011; Pisella et al., 2005; Weiner et al., 1983; Werner et al., 2010). Data from lesion studies is further supported by functional neuroimaging research demonstrating that the PPC is active early on during PA, suggesting a role in error correction (Clower et al., 1996; Danckert, Ferber, & Goodale, 2008; Luaute et al., 2009), whereas the cerebellum becomes increasingly active as PA progresses, which is indicative of a role in *spatial realignment* (Chapman et al., 2010; Danckert et al., 2008; Luaute et al., 2009).

Although it is clear that the cerebellum plays a critical role in PA, it is unclear which visual pathways to the cerebellum provide the necessary input (for a review see Glickstein, 2000). Previous work in cats and non-human primates has demonstrated that the cerebellum receives a number of projections from cortical and subcortical visual structures that process motion and are also implicated in the visual control of limb and eye movements. Specifically, cells in the superior colliculus, the motion sensitive areas MT and superior temporal sulcus (STS), as well as regions of the dorsal "vision for action" pathway in the PPC such as the intraparietal sulcus (IPS) and parieto-occipital sulcus, project to the dorsal paraflocculus, uvula,

[1] Note that an initial study by Newport and colleagues (Newport et al., 2006) failed to observe adaptation after-effects in optic ataxia patient JJ. However, a subsequent study by the same authors (Newport & Jackson, 2006) was able to demonstrate significant adaptation after-effects in JJ with his right hand using a longer prism exposure period.

paramedian lobe and Crus II of the contralateral posterior inferior cerebellum via the dorsolateral pons (Glickstein, 2000; Glickstein et al., 1980; Glickstein & Doron, 2008; Glickstein et al., 1994; Mower, Gibson, & Glickstein, 1979; Mower, Gibson, Robinson, Stein, & Glickstein, 1980). There are few (if any) visual inputs to the cerebellum from either V1 or any structures along the ventral visual pathway into the cerebellum of non-human primates and cats (Glickstein, 2000; Glickstein et al., 1980; Glickstein et al., 1994).

In humans, functional connectivity is observed between regions of the posterior inferior cerebellum and regions in the middle and superior temporal cortex and the PPC (Buckner, 2013; Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011), whereas no functional connectivity is observed between early visual areas and the cerebellum (Buckner et al., 2011). Neuropsychological work demonstrates that lesions to the posterior inferior cerebellum disrupt PA (Martin et al., 1996; Werner et al., 2010). Given the anatomical, functional, and neuropsychological evidence, it is reasonable to expect that the extrageniculostriate visual pathways to the cerebellum arising from V5/MT and the PPC contribute to PA. The current study set out to test this hypothesis.

In the current study we examined whether visual input from primary visual cortex (i.e., V1), and/or the ventral visual stream, are even necessary to adapt to prisms. Specifically, we examined PA in ‘MC’ who is clinically blind to static retinal stimulation following extensive bilateral lesions to occipital and ventral-temporal cortex. MC does, however, report dynamic retinal stimulation that arises from moving stimuli, exhibiting a kind of Riddoch phenomenon (Arcaro et al., 2018; Danckert, Tamietto, & Rossetti, in press; Riddoch, 1917). Nevertheless, other than being able to detect the state of motion in a stimulus, she seems unable to reliably extract any visual stimulus properties from her experience (Arcaro et al., 2018). Importantly,

MC's cerebellum is structurally intact, and the motion sensitive regions MT and STS are spared bilaterally, consistent with her spared motion perception (Figure 1; Arcaro et al., 2018). In addition, MC's left PPC and superior colliculus are also intact. Thus, if visual input from V1 and the ventral stream are *not* required for PA, then MC should still be able to adapt to prisms. Alternatively, if visual input from V1 and the ventral stream *are* required to adapt to prisms, then MC should show no evidence of PA.

Methods:

Participants.

Patient MC.

MC's clinical history, as well as her preserved abilities, have been documented in numerous other publications (Arcaro et al., 2018; Culham, Witt, Valyear, Dutton, & Goodale, 2008; Dutton, 2003; Snow, Goodale, & Culham, 2015; Striemer, Whitwell, & Goodale, 2017; Thaler et al., 2016; Wolf et al., 2008; Wood, Chouinard, Major, & Goodale, 2016). Briefly, MC is a right-handed female who was born in 1969 and was 48 years old at the time of testing. As a result of a severe respiratory infection at age 30 MC suffered bilateral strokes which resulted in extensive damage to her occipital lobes and ventral-temporal cortex. In addition, MC also has a lesion in her right posterior parietal cortex. Figure 1 depicts T1 weighted MRI scans of MC's brain obtained in 2011, approximately 10 years post injury. The damage to MC's ventral stream encompasses both object processing regions in the lateral occipital cortex (Snow et al., 2015), as well as face processing regions in the occipital and fusiform face areas (Striemer et al., 2017). It is important to note that, despite MC's large cortical lesions, her cerebellum is completely intact.

These extensive lesions have left MC completely blind to static stimuli during perimetry testing (Dutton, 2003; Thaler et al., 2016). However, MC can detect moving targets, and has

relatively spared motion perception, as area MT is undamaged in both hemispheres (Arcaro et al., 2018). For example, MC is capable of determining the direction of motion for square wave gratings (67% accuracy) and a single bar (90% accuracy) using a four-alternative forced-choice procedure (Arcaro et al., 2018). MC is also able to avoid obstacles even though she is unable to identify the objects she is avoiding (Arcaro et al., 2018). Although MC has some remarkable spared motion perception abilities she is unable to reliably indicate the form of these moving objects. As noted by Arcaro and colleagues (2018), "she may clearly report the experimenter's hand moving toward her, but not be able to tell reliably whether the thumb is pointing up vs. down. (p. 3)." MC has difficulty maintaining fixation (as is common in patients with cortical blindness) because she has strabismus, and also because she has no consciously accessible visual information to fixate on. Note that MC's difficulty with maintaining fixation posed no problems for her participation in the current study as all tasks were completed under free viewing.

-- Insert Figure 1 here --

In the current investigation MC was tested at her home in the United Kingdom in February of 2018. Prior to the testing session a consent form was read aloud to MC where she provided written consent. All experimental procedures were approved by the Human Research Ethics Board at MacEwan University as well as the Health Sciences Research Ethics Board at the University of Alberta. MC was compensated £10 per hour for her participation.

Controls

To compare patient MC's data to neurologically-intact adults, we tested 16 younger healthy controls (mean age=22.6; SD=2.44; 9 males; all right-handed), as well as a gender matched age-appropriate control (47-year-old female, right-handed). All control participants were tested at MacEwan University in Edmonton, Alberta, Canada. Control participants provided written informed consent, and were compensated with either course credit, or $10 per hour for their participation. All experimental procedures were approved by the MacEwan University Human Research Ethics Board.

General Procedure

During the test session, participants were seated at a table with their head in a chin rest. The table supported a horizontally mounted touch screen which was used to record touch endpoints. To measure the influence of the prisms, we administered a straight-ahead pointing task (SAP) as a measure of subjective straight-ahead (SSA) and a visual-target directed pointing task (Pointing) to measure touchpoint accuracy.

We first administered five SAP Task trials and then 20 Pointing Task trials, without any prism goggles, to establish baseline performance (termed the "*Baseline Phase*"). On each SAP trial, participants closed their eyes and then pointed straight ahead from their body midline, before touching the screen immediately below. Pointing Task trials started with the participant placing their index finger (of the left or right hand, depending on the testing session) on the "home" position. The experimenter then pressed a key which initiated a randomly selected delay of either 500, 750, 1000 or 1250ms after which a lone target was presented on the touchscreen 10° to the left or right of midline for 1-sec. The target was a square (2 x 2cm) black and white reversing checkboard that flickered at a frequency of 4Hz. Please note that previous work has

shown not only that MC can detect flicker at this frequency, but that this ability is likely due to her residual motion perception and functioning V5/MT (Arcaro et al., 2018; Striemer et al., 2017). We used a target stimulus that MC believed she could detect so that she could feel confidence in her understanding of the task instructions and her performance. Participants, including MC, were instructed to reach out to touch the target as swiftly and as accurately as they could, using their index-finger, as soon as they saw the target. The first touchpoint registered by the screen was selected as the finger endpoint for that trial. Following contact with the screen the target disappeared and the participant returned their finger to the "home" position to start the next trial. Note that vision of the hand and the target were not obstructed during the reach (i.e., concurrent feedback).

Following 20 baseline Pointing Task trials, participants completed 200 additional Pointing Task trials during the *Prism Phase*. At the outset of this phase, participants wore prism goggles (Bernell, USA) that induced a 17° visual shift, either leftward or rightward, depending on the condition. Each participant was tested in four combinations of hand (left or right) and direction of prism shift (left or right). Five SAP Task trials were administered after the first 100 Pointing Trask trials of the Prism Phase. Five additional SAP Task trials were administered immediately after the Prism Phase was complete. Following this, an additional test for spatial realignment was administered during the *Washout Phase* in which participants completed 20 additional Pointing Task trials. At the outset of the Washout Phase, the prism goggles were removed so that we could measure the extent of prism adaptation *after-effect*, a hallmark indicator of *spatial realignment*. The Washout Phase also served to minimize carry-over effects to the next condition by having participants de-adapt by completing a number of pointing trials without wearing prisms. Each phase of the Pointing Task (Baseline, Prism, and Washout)

contained an equal number of left and right targets presented in a random order. The order in which each hand was tested (and each direction of prism shift within a testing session) was counterbalanced across the control participants which also served to minimize the influence of any potential carryover effects. The general experimental procedures are summarized in Figure 2.

--Insert Figure 2 here--

Specific procedures for patient MC.

MC's test session took place over two days. MC was seated at her kitchen table with her head in a chin rest 50cm away from a 22" horizontally mounted wide screen touch screen (ELO touch systems, 60Hz refresh, 1600 x 900 resolution). The distance from the "home" position to the target was 35cm (see Figure 3). On the first day, MC's left hand was tested with left prisms in the morning and right prisms in the afternoon. On the second day, MC's right hand was tested with right prisms in the morning and left prisms in the afternoon. Within a given day, there was at least two hours between when each left/right pair of prisms were tested which included a break for lunch. This lengthy break between adaptation sessions also served to minimize potential carryover effects in MC (in addition to the pointing trials completed during the Washout Phase). Due to time constraints and participant fatigue, we terminated the final test session of second day (right hand, left prisms) after MC completed the second set of SAP trials. Thus, for this condition we can only report her baseline performance on the SAP and Baseline Phase of the Pointing Task, the first 100 Prism Phase trials, and the second set of five SAP trials as a measure of spatial realignment for this condition.

--Insert Figure 3 here--

Specific procedures for controls.

Control testing occurred at MacEwan University. During the control testing sessions participants were seated at a table with their head in chin rest 45cm away from a 32" wide screen touch screen (ELO touch systems, 60Hz refresh, 1366x768 resolution). The distance from the "home" position to the target was 35cm. All other aspects of the procedures were identical to those described for MC.

Data Processing and Statistical Analysis

For each SAP and Pointing Task trial, touchpoints were recorded as deviations along the screen's width, away from the midpoint of the screen. Thus, negative deviations reflect touchpoints that fell left of screen midpoint, whereas positive deviations reflect touchpoints that fell right of screen midpoint. For the SAP Task, negative deviations reflect a leftward-biased SSA and positive deviations a rightward-biased SSA. We computed the mean SSA for each participant and condition combination (2 prism x 2 hand), in each of the baseline and two Prism Phase sets of five SAP trials. *Spatial realignment* was indexed in each participant and condition by computing the difference between the mean baseline SSA and (1) the prism-phase midpoint mean SSA and (2) the prism-phase end mean SSA. In both cases, negative differences reflect leftward shifts in SSA, whereas positive shifts reflect rightward shifts in SSA. Spatial realignment would be evidenced by a change in SSA in the direction *opposite* the prism shift. It is important to emphasize that because post-prisms SSA was always calculated as a change from

baseline it minimized the potential for carryover effects from any previous prisms session from influencing the data. Furthermore, carryover effects were also minimized by the fact that there was a long (2-hour) break in between adaptation sessions for MC, and that the order in which the prisms sessions were tested was counterbalanced in the control participants.

For the Pointing Task, pointing deviations were converted into a measure of accuracy, *x-error*, which we computed as the distance between the center of the target (the target's x-deviation) and the touchpoint (the touchpoint's x-deviation). Thus, in the Pointing Task, negative x-error reflects touchpoints that fell left of target-center, whereas positive x-error reflect touchpoints that fell right of target-center. For each participant by condition combination, mean x-deviations were computed for the Baseline Phase set of 20 trials, the first five trials of the Prism Phase, the midpoint of the Prism phase (trials 96-100), the end of the Prism Phase (trials 196-200) and the first five trials of the Washout Phase. This allowed us to quantify four main measures of interests.

The first measure was a manipulation check. We computed the initial effect of a given combination of prism-shift and hand on baseline x-error as the difference between the mean baseline x-error and the mean x-error for the first *five* trials of the Prism Phase. Negative differences reflected left-of-target shifts in touchpoint, whereas positive shifts reflected right-of-target shifts. Thus, an *initial* prism effect would shift mean x-error *in the direction of the prisms*. Please note that the choice for five trials was guided by the desire for (1) a stable sample estimate, which would theoretically *increase* with the number of trials included and (2) a representative sample estimate of the effect of the prisms on the initial touchpoints, which would theoretically *decrease* over successive trials due to the error-minimizing effects of strategic recalibration.

The second measure was the amount of *recalibration* that occurred in the Pointing task, which we computed as the difference between the mean x-error for the first *five* trials of the Prism Phase and (1) the mean x-error at the midpoint of the Prism Phase and (2) the end of the Prism Phase. Recalibration would be evidenced by a reduction in mean x-error from the beginning, to the midpoint, to the end of the Prism Phase.

The third measure was *spatial realignment* following the Pointing task, which we indexed as the prism after-effect. After-effects were evidenced by shifts in mean x-error in the direction *opposite* the prisms. They were computed as the difference between the mean Baseline Phase x-error and the mean x-error of the first five trials of the Washout Phase.

We also supplemented these analyses of the Prism Phase x-error with a more holistic approach. This took the form of using exponential decay functions, $f(t) = \gamma + \alpha e^{-\beta t}$, for each participant and each combination of prism and hand, to model x-error as a function of trial number, *t*, and three least-squares parameter estimates: $\hat{\alpha}$, the estimated decrement in x-error due to prism adaptation; $\hat{\beta}$, an estimated coefficient to modify the trial-to-trial default proportional decrement (e, Euler's constant), in x-error at t, given x-error at $t - 1$; and, $\hat{\gamma}$, the estimated remaining x-error which, when the baseline x-error is subtracted away, reflects the estimated prism-induced x-error left remaining at the end of the Prism Phase. Notably, the model estimates the initial influence of the prism on x-error at $t = 0$ when baseline x-error is removed. This neatly avoids the issue of selecting the number of trials to include to compute mean x-error. Exponential functions were also used to model x-error from the Washout Phase for each participant for each combination of prism and hand tested. For this analysis, $\hat{\alpha}$ reflects the estimated reduction in prism after-effect; $\hat{\beta}$ is as described above; and $\hat{\gamma}$, the remaining x-error which reflects the remaining after-effect when baseline x-error is removed.

An outlier analysis was first performed on the Prism Phase x-errors within each control participant in which trials that exceeded a *t*-value of 5 *and* in which x-error exceeded 15 cm were removed over a sliding window of 30 trials. Given the effect of the prisms on vision and their after-effects on x-error, we did not subject the first 10 trials of the adaptation phase to the outlier analysis. Furthermore, because of the temporary nature of after-effects in general and because the Washout Phase lasted 20 trials, we did not subject these data to an outlier analysis. In total, the outlier analysis removed 18 trials (out of 17280) or < 0.11% of the x-error data.

Before comparing MC's performance against those of the controls, we used an independent-samples *t*-test on the baseline measures to determine whether or not the age-appropriate control was abnormal relative to the younger control group (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). For each of these tests, the alpha level was set to 0.05 to maximize statistical power to detect a difference between the age-appropriate control and the younger control group. None of the tests indicated abnormality (see supplementary Table 1), and we, therefore, grouped the age-matched control with her younger counterparts (n=17).

The effects of the prisms as described above were tested (1) on the controls using one-sample t-tests against zero or paired-samples *t*-tests where appropriate and (2) on MC using one-sample t-tests against zero or independent-samples *t*-tests assuming unequal variance. These tests were grouped into families spanning the four combinations of prism and hand and were separated by dependent measure (x-error, model estimates, or SSA), effect (the initial prism effect, extent of adaptation, the remaining effect, and the indices of spatial realignment), and group (controls or MC). Within each family of tests, the per-contrast alpha level was adjusted using the Holm step-down procedure (Holm, 1979). We tested the normality or abnormality of MC's measures by contrasting them against those of the controls using independent-samples t-

tests as was done for the age-matched control (Crawford & Garthwaite, 2002; Crawford & Howell, 1998). We increased the statistical power of these tests to detect abnormality by leaving the per-contrast alpha unadjusted. All tests were two-tailed.

Results:

General remarks about MC's test session

During the testing sessions MC could detect the presence of the flickering checkerboard target. This is consistent with earlier observations that MC is capable of detecting movement, but is unable to perceive the form of moving objects (Arcaro et al., 2018). Repeated questioning during the testing sessions indicated that she was not able to see her hand as it moved toward the target, nor could she see where her finger or hand landed with respect to the target. It is important to note that MC was never given any information about how the "special glasses" worked, or how they might influence her performance. Consistent with this, MC seemed to demonstrate little insight into how the prisms affected her performance. For instance, she remarked that the glasses seemed to "make things fuzzy," "were a bit disorienting" and "made things harder" when she tried to reach for the target. However, she never made any remarks about the glasses shifting her vision in a particular direction. Below we present the results for MC and controls separately for each phase of the experiment (i.e., Baseline, Prism Phase, Washout) for each prism shift by hand combination.

Baseline performance

Although our principal measures are each relative to baseline, Table 1 lists the baseline mean x-error and mean SSA for the control group and MC for each combination of prism and hand along

with the accompanying tests for deficit. MC's mean baseline x-errors in the Pointing Task are statistically indistinguishable from the controls in the left-prism conditions, but were biased leftward relative to the control means in the right prism conditions (1.21 cm in the left-hand condition; and 1.51 cm in the right-hand condition). MC's mean SSA departed more dramatically from the controls than did her Pointing Task touchpoints. Her mean SSA fell 11.32 cm to the left of the controls in the Left-Prism Left-Hand condition, 13.68 cm to the right in the Left-Prism Right-Hand condition, 11.52 cm to the right in the Right-Prism Right-Hand condition, and was statistically indistinguishable from the control mean in the Right-Prism Left-Hand condition (Table 1).

--Insert Table 1 here--

Figure 4 displays the full complement of x-errors and model estimated x-error for all participants for each combination of prism and hand tested. This figure nicely illustrates for each condition a number of signature features of the prism manipulation, including (1) the initial effect which biases x-error in the direction of the prism shift, (2) the gradual reduction of this bias due to strategic control, (3) remaining unresolved prism influence, (4) the prism after-effect on the initial trials of the Washout Phase in initial x-errors shift in the direction *opposite* the prisms as the prism-compensatory reach-plan persists despite the absence of prisms – the hallmark signature of spatial realignment, and (5) the return to baseline x-error as the after-effect wears off. Note that MC shows a very similar pattern with the exception of the Left Prism-Right Hand condition in which her touchpoints became more variable and biased rightward overall. Note that the patient was quite fatigued in this (last) testing session which resulted in its early

termination. Furthermore, MC's x-errors in all conditions depart substantially from the controls in terms of the extent of prism-induced error she was able to resolve, expressing a larger prism-induced bias even after 200 trials.

--Insert Figure 4 here--

Prism Phase: Initial effect of the prisms on x-error

Figure 5A shows the model estimates of the first-trial effect of the prisms for MC and the controls for each combination of prism and hand. The direction of the prism shift reliably predicts the direction of x-error for MC and the controls in all conditions except the Left-Prism Right-Hand condition in which MC's touchpoints were heavily biased to the right of the targets. The prediction intervals in the figure reveal that MC's estimated first-trial x-errors are typical for all conditions except for the Right-Prism Left-Hand condition in which MC's touchpoints were heavily biased to the right of the targets (see Table 2 for the test statistics).

Figure 5B shows the difference between mean baseline x-error and the mean x-error on the first five trials of the Prism Phase for MC and the controls for each combination of prism and hand. The direction of the prism shift reliably predicts the direction of x-error for the controls and MC in all conditions except for MC in the Left-Prism Right-Hand condition in which her touchpoints were biased to the right of the targets. The prediction intervals show that MC's shift in x-error in this condition was outside the control range, but that her x-error shifts were well within the control range for the remaining conditions (see Table 2 for the test statistics).

--Insert Figure 5 and Table 2 here--

Prism Phase: Reduction of prism-induced x-error

The extent of prism adaptation was assessed by testing the difference between the mean x-error of the first five Prism Phase trials and (1) the mean x-error of Prism Phase trials 96-100 (Figure 6A) and (2) the mean x-error of the final five trials of the Prism Phase (Figure 6B). As Figure 6A and Figure 6B each show, the mean control prism-induced x-errors were significantly reduced relative to their initial levels at both points of the Prism Phase for all conditions (compare with Figure 5B). MC reduced her mean x-errors in each combination of prism and hand tested, but the reduction was only statistically significant in the Right-Prism Left-Hand condition. However, it is important to note the prediction intervals show that the magnitude of MC's x-error reduction falls within the control range across all conditions (see Table 3 for the test statistics).

Figure 6C shows the model-estimated reduction in prism-induced x-error for MC and for the controls in each combination of prism and hand. Figure 6C makes it clear that MC and the controls significantly reduced x-error in all conditions except for the Left-Prism Right-Hand condition ($t(97)=1.94$, $p=.057$, $\alpha'=0.05$) which showed a trend, despite her rightward overall bias. The prediction intervals in Figure 6C indicate that each of MC's estimates fall within the control range (see Table 4 for the test statistics).

Figure 6D shows the model-estimated prism induced x-error left uncorrected. As this figure indicates, even after 200 trials, the prisms continued to induce a small and significant bias on the control x-error for each condition. Perhaps most salient in Figure 6D is the significant and large model-estimated bias in MC's x-error that remains uncorrected for in each condition. This bias is in the direction of the prism shift for all conditions except for the Left-Prisms Right-Hand condition in which her touchpoints were biased rightward. The prediction intervals show that

MC left significantly more bias uncorrected for than the controls did in all conditions (see Table 4 for the test statistics).

--Insert Figure 6 and Tables 3 & 4 here--

Washout Phase: Prism after-effects and spatial realignment

Figure 7A shows the model estimated first trial after-effects as the estimated x-error on the first trial of the Washout Phase. As Figure 7A indicates, the estimates are biased in the direction *opposite* the prisms in each condition tested, with the exception of MC's Right-Prism Left-Hand condition ($t(17)=-1.3$, $p > .19$, $\alpha'=0.05$). Figure 7A also shows that MC's estimated first-trial x-error falls within the control range for each condition tested (see Table 5 for the test statistics).

Figure 7B shows the after-effects using the difference between the mean baseline x-error and the mean of the first five trials of the Washout Phase. Figure 7B makes it clear that both MC's means and those of the controls show significant shifts in the direction *opposite* the prisms, consistent with prism after-effects of spatial realignment. Figure 7B also shows that MC's shifts fall within the control ranges in each of the conditions tested (see Table 5 for the test statistics).

--Insert Figure 7 and Table 5 here--

Subjective straight ahead (SSA) and spatial realignment

Figure 8 shows spatial realignment for MC and the controls as indexed by the difference between the mean baseline SSA and the mean SSA from the SAP trials at the midpoint (Figure 8A) and end (Figure 8B) of the Prism Phase for each combination of prism and hand. As Figure 8A and

Figure 8B clearly show, the mean control SSAs shift in directions consistent with spatial realignment at both points of the Prism Phase. For rightward prism-shifts, MC's mean SSAs were consistent with the effects of spatial realignment at the midpoint for both the left hand and the right hand, yet only the left hand mean SSAs remained this way by the end of the Prism Phase. For left prisms, MC's mean left-hand SSAs were not consistent with spatial realignment at either the midpoint or end of the Prism Phase, whereas her mean SSAs with her right hand were consistent with spatial realignment at the midpoint before testing in that condition ended after 100 trials due to time constraints and patient fatigue (see Table 6 for the test statistics).

--Insert Figure 8 and Table 6 here--

Discussion:

The primary question posed in this study was whether an intact V1 and surrounding early visual cortex are necessary for adaptive visuomotor control. We addressed this question by testing 'MC,' who is blind to static stimuli following bilateral lesions to occipital and ventral-temporal cortex, on a prism adaptation task. We also repeated the experiment with neurologically intact and normally-sighted controls in order to determine the normality/abnormality of MC's performance. Not surprisingly, both the age-appropriate control (Supplementary Table 1) and the combined control group (i.e., the younger controls combined with the age-appropriate control) had no trouble adapting to each prism shift by hand combination. Specifically, control participants demonstrated both *strategic recalibration*, by reducing their pointing errors during adaptation (Figure 6), and *spatial realignment*, as indexed by prism after-effects (Figures 7-8). This means that healthy control participants perseverated by pointing in the direction opposite the prism shift in the Washout Phase of the procedure (Figure 7).

Remarkably, MC demonstrated evidence of strategic recalibration by reducing her pointing errors by the same magnitude as controls for all prism shift by hand combinations (Figures 6A & 6B). That is, although MC only showed statistically significant pointing error reduction at the individual subject level for the Left Hand-Right Prisms condition (Figure 6A & B), the magnitude of MC's x-error reduction fell within the control range across all conditions. More importantly, MC exhibited *spatial realignment* – the hallmark signature of adaptation – as indexed by shifts in (1) pointing errors in the direction opposite the prisms in the Washout Phase (Figure 7) in all three of the prism shift by hand combinations that we were able to test (i.e., Right Prisms-Right Hand, Right Prisms-Left Hand, Left Prisms-Left Hand) and (2) SSA in the direction opposite the prisms as measured by SAP for both the Right Prisms-Right Hand and Left Prisms-Right Hand conditions (Figure 8). In short, patient MC showed some form of adaptation (i.e., demonstrated a significant prism after-effect) to both a leftward and a rightward prism shift using either her right or left hand, despite having extensive lesions that prevented input from the geniculostriate visual pathway. In summary, while previous studies have demonstrated that patients with unilateral occipital lesions (i.e., with one intact visual field) could adapt to prisms with somewhat reduced after-effects (Weiner et al., 1983), the current data clearly demonstrate, for the first time, that it is possible to adapt to prisms in the absence of any visual input from V1 and surrounding early visual cortex.

It is important to note that the target locations that were used during the Washout Phase post PA were the same locations used during the Prism Phase itself. Although this is a common design choice for prism adaptation experiments (for a review see Redding et al., 2005), it is possible that the target locations cue some sort of motor memory of previously recalibrated pointing movements. Indeed, after-effects can be larger when the same target location is used.

Thus, the after-effects measured in the Pointing Task may index a *combination* of recalibration and realignment (Redding et al., 2005). This cannot be so for the SSA measures taken from the SAP Task administered here. According to those measures, the controls, and even MC in the right-prism condition exhibited spatial realignment. Taken together, the data leads us to conclude that spatial realignment was in fact contributing to the after-effects observed here.

One important question raised by the current study is how MC was able to compensate for prism-induced pointing errors in the absence of a consciously available error signal. One intuitive answer involves cross-modal comparison between tactile, kinesthetic, and proprioceptive sources of sensory feedback about the limb's performance and the visual estimate of the target's position. Indeed, healthy adults are able to adapt to prisms, despite being unaware of any visual shift or terminal error that was induced by the prisms (e.g., Jakobson & Goodale, 1989; Michel, Pisella, Prablanc, Rode, & Rossetti, 2007). Furthermore, it is well-known that healthy participants can amend their reach to a sudden change in target location even when they are not able to consciously report the change in target position (Goodale, Pelisson, & Prablanc, 1986; Pelisson, Prablanc, Goodale, & Jeannerod, 1986). More importantly, our findings suggest that the geniculostriate pathway is not necessary for the generation and processing of visual error signals. Indeed, they imply that the visual guidance that underlies MC's intact PA is supported by intact extrageniculate pathways to MT/V5. Such pathways might include regions such as MT and the PPC, which receive extrageniculo retinal input via the superior colliculus (Lyon, Nassi, & Callaway, 2010) and inferior pulvinar (Kaas & Lyon, 2007). MT also receives visual input from the koniocellular pathway (via short wavelength S-cones) through connections with the lateral geniculate nucleus which also bypass V1 (Sincich, Park, Wohlgemuth, & Horton, 2004). In the absence of V1, the scaling of in-flight grip aperture to target size during grasping in cases

of action blindsight has been argued to be served by the extrageniculostriate pathway through a demonstrably functioning V5/MT (Whitwell, Striemer, Nicolle, & Goodale, 2011). Indeed, previous work with MC has demonstrated that she has preserved motion perception because the motion sensitive regions MT and STS are spared bilaterally (Arcaro et al., 2018). If we assume that MC's MT and PPC are receiving subcortical visual inputs through the superior colliculus and pulvinar, or lateral geniculate nucleus (via the koniocellular pathway), then MT and the PPC could relay visual signals to the posterior inferior cerebellum through their known connections with the dorsolateral pons (Glickstein, 2000; Glickstein et al., 1980; Glickstein & Doron, 2008; Glickstein et al., 1994).

Although MC demonstrated clear after-effects for each hand by prism shift combination, her performance was not typical for every facet of the study. For example, she seemed to have more difficulty adapting to left prisms when using her right hand. In this condition, her touchpoints were highly variable and biased to the right of the targets (see Figure 4). Furthermore, MC did not demonstrate a significant shift in SSA when adapting to left prisms with the left hand. One simple explanation for this observation is a possible "field effect" stemming from damage to MC's right PPC. Specifically, MC's right PPC lesion includes damage to the precuneus (BA19), superior parietal lobule (SPL; BA5) and intraparietal sulcus (IPS) with some extension into supramarginal gyrus (BA40) of the inferior parietal lobe (Figure 1; Arcaro et al., 2018; Wood et al., 2016). These PPC regions are important for controlling attention (for a review see Corbetta & Shulman, 2002) and visually guided actions such as reaching, grasping, and eye movements (e.g., Astafiev et al., 2003; Buneo & Andersen, 2006; Culham, Cavina-Pratesi, & Singhal, 2006; Culham & Valyear, 2006; Milner & Goodale, 2006). Indeed, damage to the PPC can result in optic ataxia, a disorder in which patients have difficulty

with reaching towards and grasping objects in contralesional space (Karnath & Perenin, 2005; Perenin & Vighetto, 1988; Pisella et al., 2009; Pisella et al., 2007). Interestingly, previous studies have demonstrated that, although patients with optic ataxia following PPC lesions often require more trials to reduce their pointing errors, they are still able to produce after-effects (Newport & Jackson, 2006; Pisella et al., 2004; Striemer et al., 2008).

Given (1) the importance of the PPC in attention and visually-guided action and (2), MC's right PPC lesion, it is perhaps not surprising that she had more difficulty adapting to leftward shifting prisms, as this condition would have shifted her vision towards her contralesional (and possibly ataxic) field. This is also consistent with an interesting observation in Rossetti's seminal (1998) PA study in which he noted that patients with neglect with right hemisphere lesions were easily able to adapt to rightward shifting prisms, but had difficulty adapting to leftward shifting prisms (see also Luaute et al., 2012). Despite MC having a little more difficulty adapting to leftward shifting prisms overall, it is important to reiterate that she showed clear after-effects (i.e., spatial realignment) to leftward and rightward shifting prisms with both the left and right hand as measured by SSA and/or pointing during the Washout Phase.

Another atypical aspect of MC's data is that it included greater uncorrected prism-induced pointing errors compared to controls following the 200 Prism Phase pointing trials. That is, even though MC adapted to prisms in each condition (i.e., she demonstrated significant after-effects), she failed to compensate for the prism shift to the same extent (Figure 6D). This is consistent with previous work demonstrating that unilateral lesions that extend into the occipital lobe may result in reduced recalibration during PA, and reduced after-effects following PA (Serino, Angeli, Frassinetti, & Ladavas, 2006; Weiner et al., 1983). However, in each of these previous studies the patients were only affected by unilateral vision loss (i.e., hemianopia or

quadrantanopia) and thus retained conscious vision in one visual hemifield which allowed conscious knowledge of reach errors during adaptation. Our study is the first to demonstrate that it is possible to adapt to prisms without *any* input from V1 or early ventral stream areas.

In summary, these data indicate that visual input from occipital cortex (including V1) and other foundational structures of the ventral stream are not necessary for spatial realignment to occur. Instead, we surmise that the extrageniculostriate pathway through V5/MT is capable of providing the cerebellum and PPC with the necessary input for visuomotor adaptation as well as motor learning. To conclude, while we do not claim that V1 and early visual areas make *no* contribution to visuomotor adaptation, these data clearly show that these structures are *not necessary* for visuomotor adaptation.

Acknowledgements:

This research was funded through a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant (RGPIN-2014-04542) awarded to CS, an NSERC Discovery Grant (RGPIN-2013-36796) awarded to JTE, and an NSERC Postdoctoral Fellowship awarded to RLW. The authors are grateful to Brittany Angus-Cook and Adam Morrill for their assistance collecting the control data. The authors are also grateful to Drs. Jorn Diedrichsen and Paul Gribble for conversation and guidance concerning modelling and to their source for support (Canada First Research Excellence Fund, BrainsCAN, to The University of Western Ontario's Computational Core at the Brain and Mind Institute). Finally, the authors are especially grateful to MC and her husband for their time and hospitality during the testing sessions.

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Table 1. Baseline mean (standard deviation and within-subject standard error italicized each in parentheses) x-error from the center of the target from the Pointing Task, in cm, and the Baseline mean subjective straight ahead (SSA) as x-deviations from the midpoint of the screen from the SAP task, also in cm, for the controls and for MC for each of the four combinations of prism shift and hand. Significant tests for abnormality are in bold.

Measure	Group and tests for abnormality	Left prisms Left hand	Left prisms Right hand	Right prisms Left hand	Right prisms Right hand
x-error	Controls	-.38 (.7)	-.18 (.39)	.64 (.42)	.38 (.41)
	MC	-.7 (*.15*)	-.97 (*.07*)	-1.09 (*.14*)	-1.08 (*.15*)
	MC vs. Controls	t=-.48, p>.63	t=-1.91, p>.07	**t=-2.56, p<.03**	**t=-3.22, p<.006**
SSA	Controls	-.74 (1.83)	-1.65 (3.25)	2.81 (2.6)	1.9 (3.22)
	MC	-12.06 (*3.14*)	12.03 (*.9*)	3.94 (*1.18*)	13.43 (*.43*)
	MC vs. Controls	**t=-6.02, p<2×10^{-5}**	**t=4.09, p<9×10^{-4}**	**t=3.47, p<4×10^{-4}**	**t=.42, p >.67**

Table 2. Pointing Task tests of statistical significance for the prism-induced x-error shifts from Baseline using (1) the initial five trials of the Prism Phase (*Mean-estimates*) and (2) the model-estimated prism-induced x-error on the first trial of the Prism Phase (*Model-estimates*) for the controls and for MC. **Non-significant tests bolded.** *MC's pointing errors were heavily biased to the right in the Prism Phase of this condition.

Condition	Group and test for abnormality	Mean-estimates	Model-estimates
Left prisms Left hand	Controls	$t(16)=-7.32$, $p<2\times10^{-6}$, $\alpha'=.025$	$t(16)=-9.56$, $p<3\times10^{-8}$, $\alpha'=.0167$
	MC	$t(4)=-6.76$, $p<.003$, $\alpha'=.0167$	$t(197)=-27.6$, $p<2\times10^{-69}$, $\alpha'=.0167$
	MC vs. Controls	**$t(16)=-.75$, $p>.46$**	**$t(16)=-.01$, $p>.98$**
Left prisms Right hand*	Controls	$t(16)=-6.42$, $p<9\times10^{-6}$, $\alpha'=.05$	$t(16)=-7.51$, $p<7\times10^{-7}$, $\alpha'=.05$
	MC	**$t(16)=1.85$, $p>.13$, $\alpha'=.05$**	$t(97)=1.91$, $p>0.057$, $\alpha'=.05$
	MC vs. Controls	$t(16)=3.61$, $p<.003$	$t(16)=3.04$, $p < .008$
Right prisms Left hand	Controls	$t(16)=9.25$, $p<8\times10^{-8}$, $\alpha'=.0125$	$t(16)=13.54$, $p<2\times10^{-10}$, $\alpha'=.0125$
	MC	$t(5)=13.61$, $p<8\times10^{-5}$, $\alpha'=.0125$	$t(195)=6.47$, $p<8\times10^{-10}$, $\alpha'=.0167$
	MC vs. Controls	**$t(16)=.31$, $p>.76$**	**$t(16)=-.43$, $p>.67$**
Right prisms Right hand	Controls	$t(16)=8.82$, $p<2\times10^{-7}$, $\alpha'=.0167$	$t(16)=9.27$, $p<4\times10^{-8}$, $\alpha'=.025$
	MC	$t(4)=3.64$, $p<.022$, $\alpha'=.025$	$t(197)=5.19$, $p<6\times10^{-7}$, $\alpha'=.025$
	MC vs. Controls	**$t(16)=.49$, $p>.62$**	**$t(16)=1.48$, $p>.15$**

Table 3. Pointing Task tests of statistical significance for the reductions in initial (first five trials) prism-induced x-error using (1) trials 96-100 of the Prism Phase (*Prism Phase midpoint*) and (2) trials 196-200 of the Prism Phase (*Prism Phase final*) for the controls and for MC**.** Non-significant tests bolded. *MC's pointing errors were heavily biased to the right in the Prism Phase of this condition.

Condition	Group and test for abnormality	Prism Phase midpoint (trials 96-100)	Prism Phase final (trials 196-200)
Left prisms Left hand	Controls	$t(16)=7.44$, $p<2\times10^{-6}$, $\alpha'=.025$	$t(16)=6.86$, $p<4\times10^{-6}$, $\alpha'=.025$
	MC	$\mathbf{t(5)=3.36, p>.019, \alpha'=.0167}$	$\mathbf{t(4)=3.21, p>.03, \alpha'=.025}$
	MC vs. Controls	$\mathbf{t(16)=-.22, p>.82}$	$\mathbf{t(16)=-.47, p>.64}$
Left prisms Right hand*	Controls	$t(16)=5.75$, $p<4\times10^{-5}$, $\alpha'=.05$	$t(16)=6.05$, $p<2\times10^{-5}$, $\alpha'=.05$
	MC	$\mathbf{t(5)=2.04, p>.09, \alpha'=.025}$	n/a
	MC vs. Controls	$\mathbf{t(16)=-.06, p>.95}$	n/a
Right prisms Left hand	Controls	$t(16)=-8.65$, $p<2\times10^{-7}$, $\alpha'=.0125$	$t(16)=-8.65$, $p<2\times10^{-7}$, $\alpha'=.0125$
	MC	$t(8)=-3.5$, $p<.009$, $\alpha'=.0125$	$t(7)=-5.44$, $p<9\times10^{-4}$, $\alpha'=.0167$
	MC vs. Controls	$\mathbf{t(16)=-.6, p>.55}$	$\mathbf{t(16)=.93, p>.36}$
Right prisms Right hand	Controls	$t(16)=-8.62$, $p<3\times10^{-7}$, $\alpha'=.0167$	$t(16)=-8.62$, $p<3\times10^{-7}$, $\alpha'=.0167$
	MC	$\mathbf{t(5)=-1.6, p>.17, \alpha'=.05}$	$\mathbf{t(4)=-1.15, p>.28, \alpha'=.05}$
	MC vs. Controls	$\mathbf{t(16)=-.43, p>.67}$	$\mathbf{t(16)=.89, p>.38}$

Table 4. Pointing Task tests of statistical significance for the model-estimated (1) reductions in prism-induced x-error across the Prism Phase (*Model-estimated adaptation*) and (2) the extent of prism-induced x-error remaining (*Model-estimated remaining x-error*) for the controls and for MC. Non-significant tests bolded. *MC's pointing errors were heavily biased to the right in the Prism Phase of this condition.

Condition	Group and test for abnormality	Model-estimated adaptation	Model-estimated remaining x-error
Left prisms Left hand	Controls	$t(16)=9.25$, $p<5\times10^{-8}$, $\alpha'=.0167$	$t(16)=-3.68$, $p<.002$, $\alpha'=.05$
	MC	$t(197)=-17.16$, $p<6\times10^{-41}$, $\alpha'=.0125$	$t(197)=-27.44$, $p<4\times10^{-69}$, $\alpha'=.0167$
	MC vs. Controls	**$t(16)=-.86$, $p>.4$**	$t(16)=-8.15$, $p<5\times10^{-7}$
Left prisms Right hand*	Controls	$t(16)=7.34$, $p<9\times10^{-7}$, $\alpha'=.05$	$t(16)=-3.8$, $p<8\times10^{-4}$, $\alpha'=.025$
	MC	**$t(97)=-1.94$, $p>.05$, $\alpha'=.05$**	$t(97)=3.98$, $p<1\times10^{-4}$, $\alpha'=.05$
	MC vs. Controls	**$t(16)=-.41$, $p>.68$**	$t(16)=29.3$, $p<3\times10^{-15}$
Right prisms Left hand	Controls	$t(16)=-13.3$, $p<3\times10^{-10}$, $\alpha'=.0125$	$t(16)=4.08$, $p<5\times10^{-4}$, $\alpha'=.0167$
	MC	$t(195)=2.58$, $p<.011$, $\alpha'=.0167$	$t(195)=46.84$, $p<1\times10^{-109}$, $\alpha'=.0125$
	MC vs. Controls	**$t(16)=2.01$, $p>.06$**	$t(16)=10.9$, $p<9\times10^{-9}$
Right prisms Right hand	Controls	$t(16)=-8.82$, $p<8\times10^{-8}$, $\alpha'=.025$	$t(16)=5.72$, $p<2\times10^{-5}$, $\alpha'=.0125$
	MC	$t(197)=3.64$, $p<.022$, $\alpha'=.025$	$t(197)=21.38$, $p<4\times10^{-53}$, $\alpha'=.025$
	MC vs. Controls	**$t(16)=-.48$, $p>.64$**	$t(16)=14.39$, $p<2\times10^{-10}$

Table 5. Pointing Task tests of statistical significance of the after-effects using (1) the difference between the mean baseline x-error and the mean x-error on the first five trials of the Washout Phase (*Mean-estimated after-effect*) and (2) the model estimates of the first trial of the Washout Phase (*model-estimated after-effect*). Non-significant tests bolded. *MC's pointing errors were heavily biased to the right in the Prism Phase of this condition.

Condition	Group and test for abnormality	Mean-estimated after-effect	Model-estimated after-effect
Left prisms Left hand	Controls	$t(16)=6.95$, $p<4\times10^{-6}$, $\alpha'=.025$	$t(16)=7.45$, $p<7\times10^{-7}$, $\alpha'=.0167$
	MC	$t(10)=10.85$, $p<7\times10^{-7}$, $\alpha'=.0125$	$t(17)=7.19$, $p<2\times10^{-11}$, $\alpha'=.0167$
	MC vs. Controls	$\mathbf{t(16)=-.39,\ p>.72}$	$\mathbf{t(16)=-.69,\ p>.49}$
Left prisms Right hand*	Controls	$t(16)=6.77$, $p<5\times10^{-6}$, $\alpha'=.05$	$t(16)=5.82$, $p<2\times10^{-5}$, $\alpha'=.05$
	MC	n/a	n/a
	MC vs. Controls	n/a	n/a
Right prisms Left hand	Controls	$t(16)=-6.92$, $p<4\times10^{-6}$, $\alpha'=.0125$	$t(16)=-6.38$, $p<5\times10^{-6}$, $\alpha'=.025$
	MC	$t(6)=-3.1$, $p<.02$, $\alpha'=.05$	$\mathbf{t(17)=-1.3,\ p>.16,\ \alpha'=.05}$
	MC vs. Controls	$\mathbf{t(16)=1.23,\ p>.28}$	$\mathbf{t(16)=1.06,\ p>.3}$
Right prisms Right hand	Controls	$t(16)=-6.8$, $p<5\times10^{-6}$, $\alpha'=.0167$	$t(16)=-7.8$, $p<4\times10^{-7}$, $\alpha'=.0125$
	MC	$t(4)=-5.44$, $p<.003$, $\alpha'=.025$	$t(17)=-5.68$, $p<5\times10^{-8}$, $\alpha'=.025$
	MC vs. Controls	$\mathbf{t(16)=.63,\ p>.55}$	$\mathbf{t(16)=.74,\ p>.47}$

Table 6. SAP Task tests of statistical significance of spatial realignment using the difference between the mean Baseline subjective straight-ahead (SSA) and (1) the mean SSA of the SAP trials administered after trial 100 of the Prism Phase (*Prism Phase midpoint*) and (2) the mean SSA of the SAP trials administered after trial 200 of the Prism Phase (*Prism Phase end)* for the controls and for MC. Non-significant tests bolded. *MC's pointing errors were heavily biased to the right in the Prism Phase of this condition.

Condition	Group	Prism Phase midpoint	Prism Phase end
Left prisms Left hand	Controls	$t(16)=7.92$, $p<6.3\times10^{-7}$, $\alpha'=.0167$	$t(16)=7.22$, $p<3\times10^{-6}$, $\alpha'=.0167$
	MC	**$t(6)=-1.11$, $p>.3$, $\alpha'=.05$**	**$t(5)=-.28$, $p>.79$, $\alpha'=.05$**
	MC vs. Controls	$t(16)=-3.45$, $p<.004$	**$t(16)=-2.01$, $p>.06$**
Left prisms Right hand*	Controls	$t(16)=3.03$, $p<.008$, $\alpha'=.025$	$t(16)=3.01$, $p<.009$, $\alpha'=.025$
	MC	$t(5)=6.64$, $p<.001$, $\alpha'=.0167$	n/a
	MC vs. Controls	$t(16)=2.32$, $p<.04$	n/a
Right prisms Left hand	Controls	**$t(16)=-2.06$, $p>0.056$, $\alpha'=.05$**	$t(16)=-2.7$, $p<0.02$, $\alpha'=.05$
	MC	$t(6)=-5.97$, $p<9\times10^{-4}$, $\alpha'=.0125$	$t(5)=-5.61$, $p<.003$, $\alpha'=.0167$
	MC vs. Controls	$t(16)=-2.65$, $p<.02$	**$t(16)=-1.84$, $p>.08$**
Right prisms Right hand	Controls	$t(16)=-7.95$, $p<6.1\times10^{-7}$, $\alpha'=.0125$	$t(16)=-7.9$, $p<7\times10^{-7}$, $\alpha'=.0125$
	MC	$t(4)=-4.48$, $p<.01$, $\alpha'=.025$	**$t(4)=1.43$, $p>.22$, $\alpha'=.025$**
	MC vs. Controls	**$t(16)=.48$, $p>.64$**	$t(16)=2.98$, $p<.009$

Supplementary Table 1. Age-matched control tests of abnormality that yielded the maximum t-score across the four combinations of prism and hand for each measure, task, and phase of the experiment.

Measure (Task)	Phase (trials)	Test for abnormality
x-error and x-error shifts (Pointing)	Baseline	$t(15)=.1$, $p>0.92$
	$\text{Prism}_{\text{(trials 1-5)}}$ vs. Baseline	$t(15)=.41$, $p>0.68$
	$\text{Prism}_{\text{(trials 1-5)}}$ vs. $\text{Prism}_{\text{(trials 96-100)}}$	$t(15)=-.6$, $p>0.55$
	$\text{Prism}_{\text{(trials 1-5)}}$ vs. $\text{Prism}_{\text{(trials 196-200)}}$	$t(15)= -.42$, $p>0.68$
	$\text{Washout}_{\text{(trials 1-5 vs. baseline)}}$	$t(15)=.31$, $p>0.76$
Model estimated x-error and x-error shifts (Pointing)	$\text{Prism}_{\text{(trial 1)}}$	$t(15)=.32$, $p>0.75$
	$\text{Prism}_{\text{(effect corrected for)}}$ $(\hat{a})$	$t(15)=-.79$, $p>0.44$
	$\text{Prism}_{\text{(effect remaining)}}$ $(\hat{\gamma})$	$t(15)=.23$, $p>0.82$
	$\text{Washout}_{\text{(trial 1)}}$	$t(15)=.17$, $p>0.86$
Subjective straight ahead (SAP)	Baseline	$t(15)=-.74$, $p>0.47$
	$\text{Prism}_{\text{(midpoint)}}$	$t(15)=2.02$, $p>0.06$
	$\text{Prism}_{\text{(end)}}$	$t(15)=1.04$, $p>0.36$

Figure captions

Figure 1: T1 weighted MRI scans depicting the extent of patient MC's bilateral lesions to occipital and ventral-temporal cortex. MC also has damage to her right PPC. Note that despite her large lesions, MC's cerebellum is completely intact.

Figure 2. Depicts the sequence of events in each prism adaptation session for the controls and for patient MC. These procedures were repeated for each prism (left vs. right) by hand (left vs. right) combination.

Figure 3. Depicts the task setup for patient MC. During the prism adaptation testing sessions MC was seated at her kitchen table in front of a 22" widescreen touch screen with her head in a chin rest.

Figure 4. x-error (dots) and model estimated x-error (traces) on each trial for MC (red), the age-matched control (blue) and the remaining controls (black) on each trial for each combination of prism and hand (separate panels). Baseline and Washout Phases, in which participants do not wear prisms, are highlighted in light purple, while the Prism Phase is highlighted in light green. The age-matched control's x-errors are statistically indistinguishable from the younger control group, showing the typical pattern of x-error bias in the direction of the prism shift on the initial trials of the prism phase. MC's x-errors are similarly biased by the prisms, except she does not compensate for their influence as much as the controls do. Furthermore, in the left prism right hand condition, the final condition tested after two days of testing, MC's touchpoints were highly variable and heavily biased to the right of the target. In the conditions tested, both the controls and MC show after-effects in which x-errors are biased in the direction opposite the prism shift on the initial trials of the Washout Phase when participants are no longer wearing the prisms.

Figure 5. The effect of the prisms as assessed by (A) model-estimated x-error on the first prism trial and (B) the difference between the mean baseline x-error and the mean of the x-error on the first five prism trials. In each panel, the error bars around the control means and MC's x-error scores reflect multiple-comparisons adjusted confidence intervals for visual tests against a null difference. Thus, intervals that do not overlap zero reflect significant differences. The bars between the controls and MC's x-error centered next to the control mean are prediction intervals for a visual test of the normality or abnormality of MC's x-error. MC's scores that fall outside this interval are abnormal.

Figure 6. The extent and direction of reduction in prism-induced x-error (i.e. adaptation) during the Prism Phase as assessed by (A) computing the difference between the mean x-error on the first five prism trials and the mean x-error on the prism trials 96-100 (the midpoint), (B) the difference between the mean x-error on the first give prism trials and the mean x-error on the final five prism trials (trials 196-200), and (C) the model. (D) Model-estimated prism-induced x-error that remains despite 200 Prism Phase trials. Error bars afford the same types of inferences as described in the caption for Figure 5.

Figure 7. After effects as assessed by (A) model estimated x-error on the first trial of the Washout Phase and (B) computing the difference between mean baseline x-errors and the mean

x-errors of the first five trials of the Washout Phase. Error bars afford the same types of inferences as described in the caption for Figure 5.

Figure 8. Spatial realignment as assessed by the difference between mean baseline SSA and (A) the mean SSA taken from the SAP Trials administered at the midpoint of the Prism Phase (after trial 100) and (B) the mean SSA taken from the SAP Trials administered at the end of the Prism Phase. Error bars afford the same types of inferences as described in the caption for Figure 5.

Figure 1.

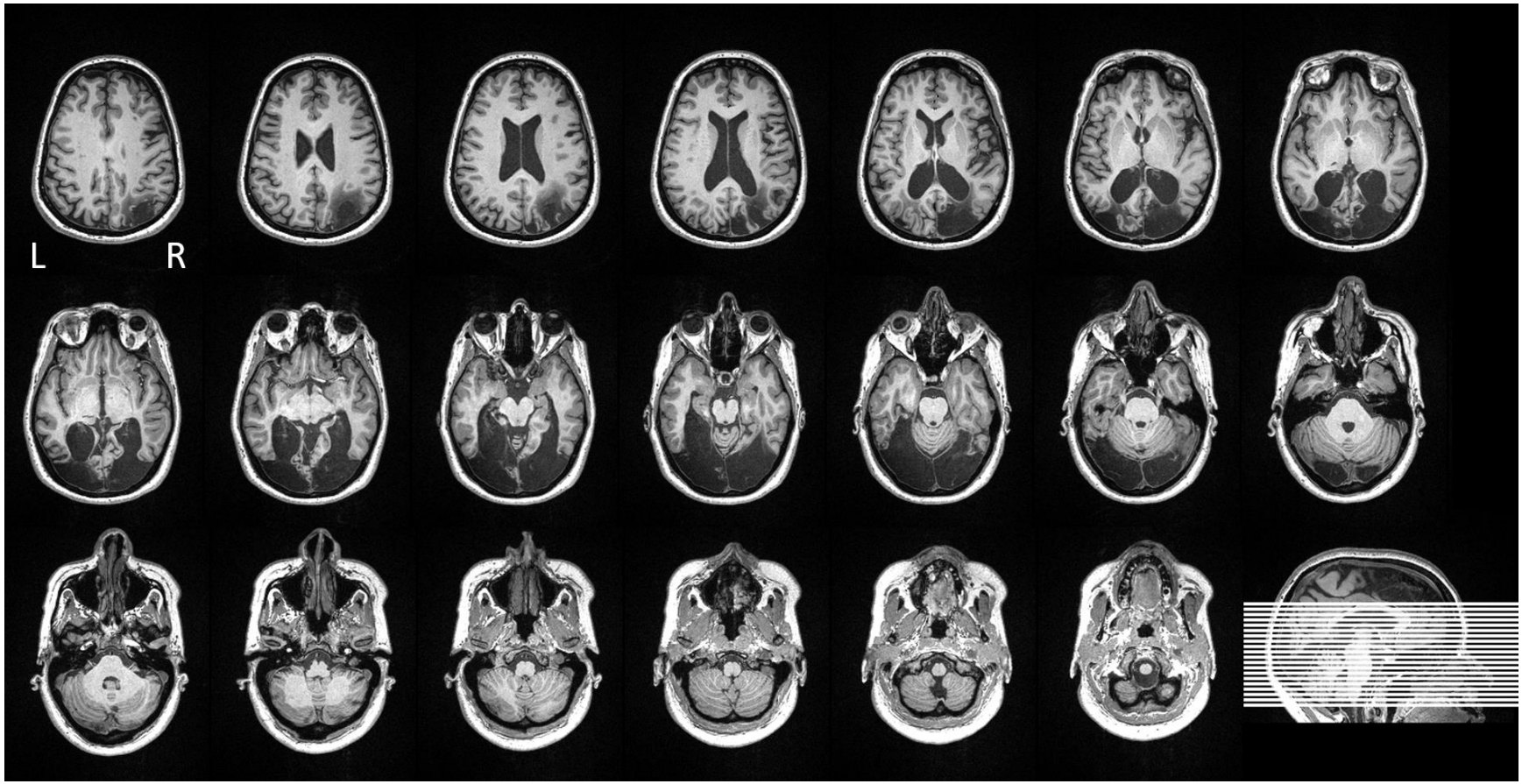


Figure 2.

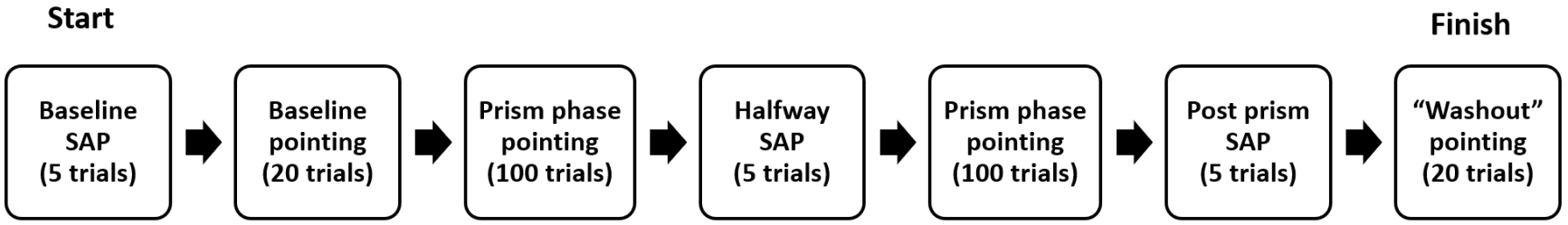

Start
Finish
Baseline SAP (5 trials)
Baseline pointing (20 trials)
Prism phase pointing (100 trials)
Halfway SAP (5 trials)
Prism phase pointing (100 trials)
Post prism SAP (5 trials)
“Washout” pointing (20 trials)

Figure 3.

Figure 4.

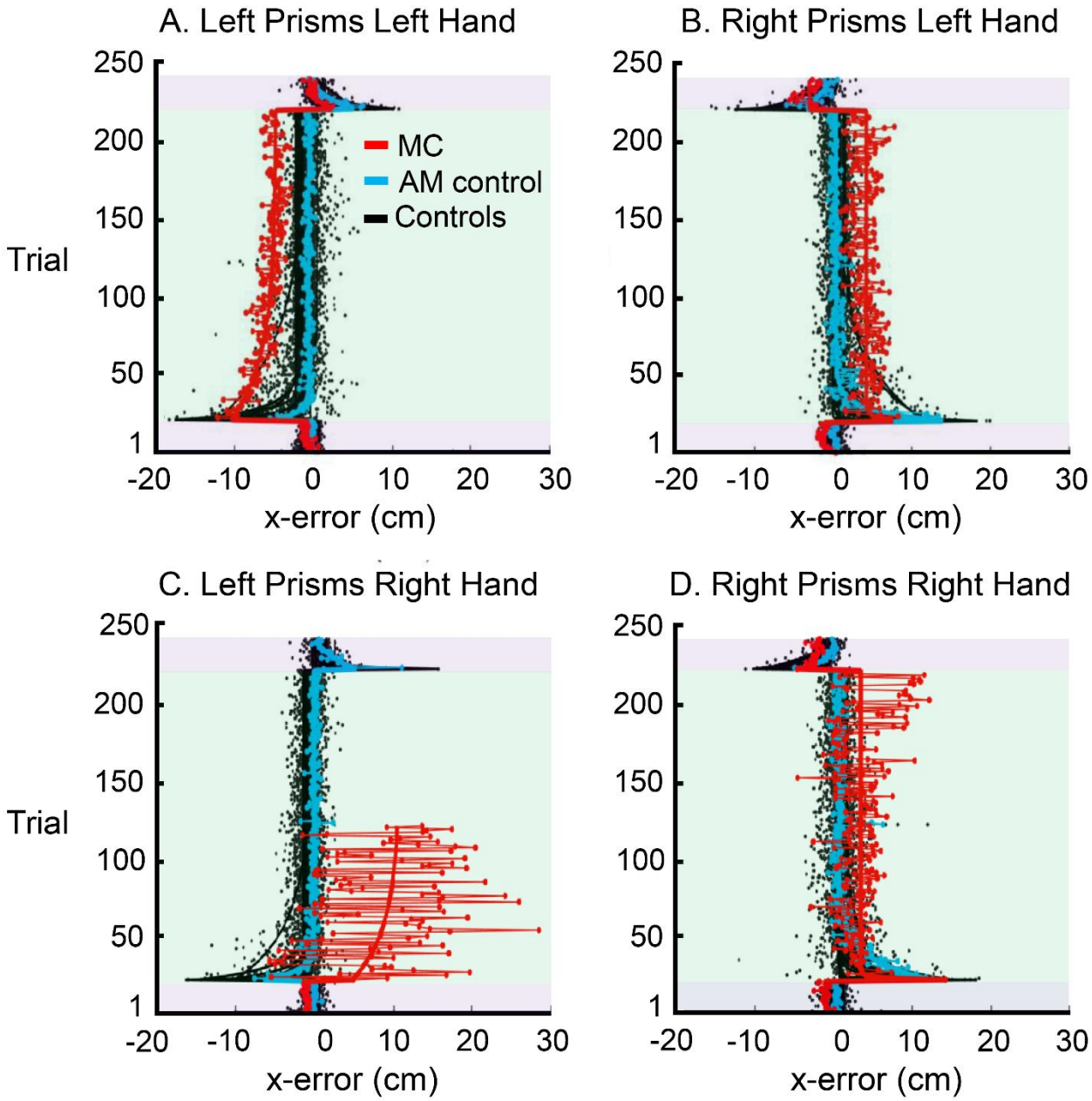

A. Left Prisms Left Hand
B. Right Prisms Left Hand
C. Left Prisms Right Hand
D. Right Prisms Right Hand
MC
AM control
Controls
Trial
x-error (cm)
250
200
150
100
50
1
-20
-10
0
10
20
30

Figure 5.

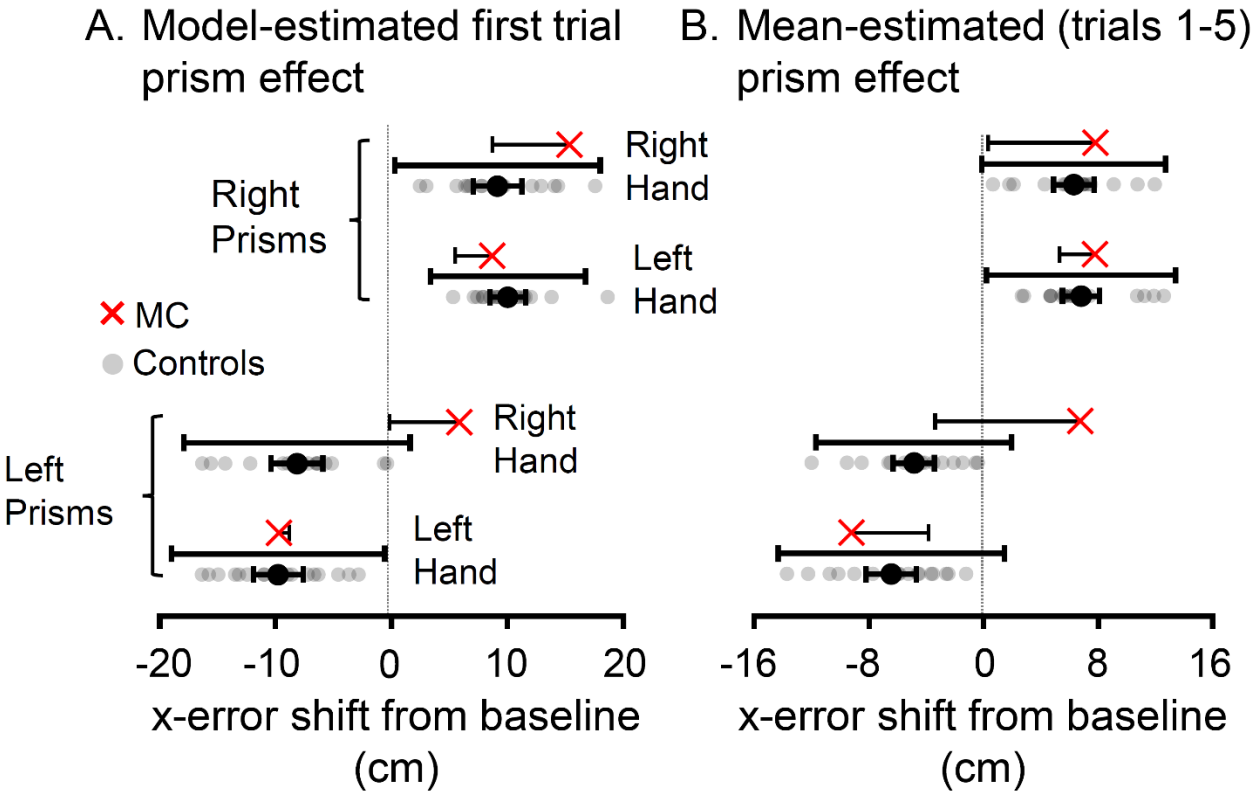

A. Model-estimated first trial prism effect
B. Mean-estimated (trials 1-5) prism effect
Right Prisms
Left Prisms
Right Hand
Left Hand
MC
Controls
-20
-10
0
10
20
-16
-8
0
8
16
x-error shift from baseline (cm)

Figure 6.

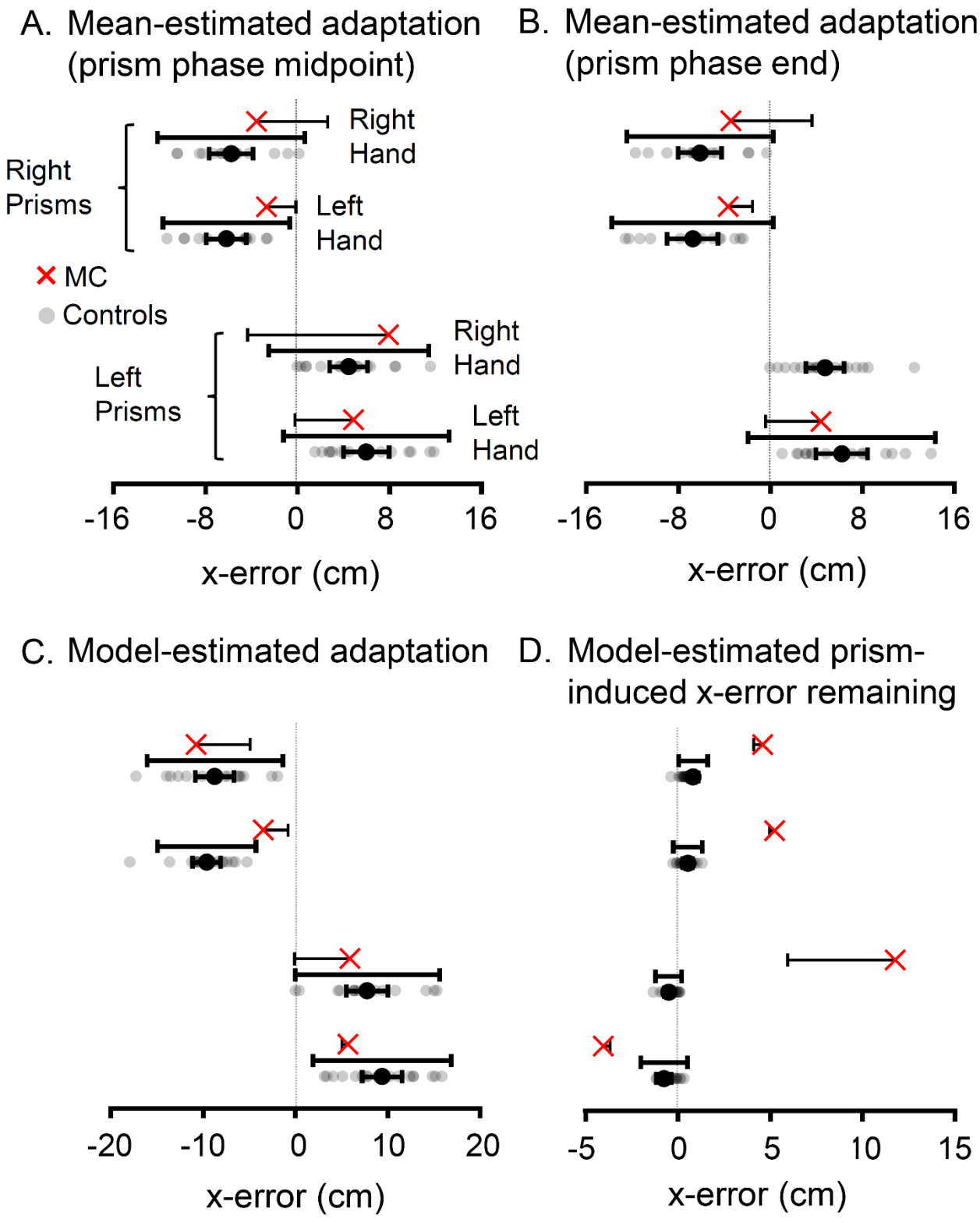

A. Mean-estimated adaptation (prism phase midpoint)
Right Prisms
Right Hand
Left Hand
MC
Controls
Left Prisms
Right Hand
Left Hand
-16
-8
0
8
16
x-error (cm)
B. Mean-estimated adaptation (prism phase end)
-16
-8
0
8
16
x-error (cm)
C. Model-estimated adaptation
-20
-10
0
10
20
x-error (cm)
D. Model-estimated prism-induced x-error remaining
-5
0
5
10
15
x-error (cm)

Figure 7.

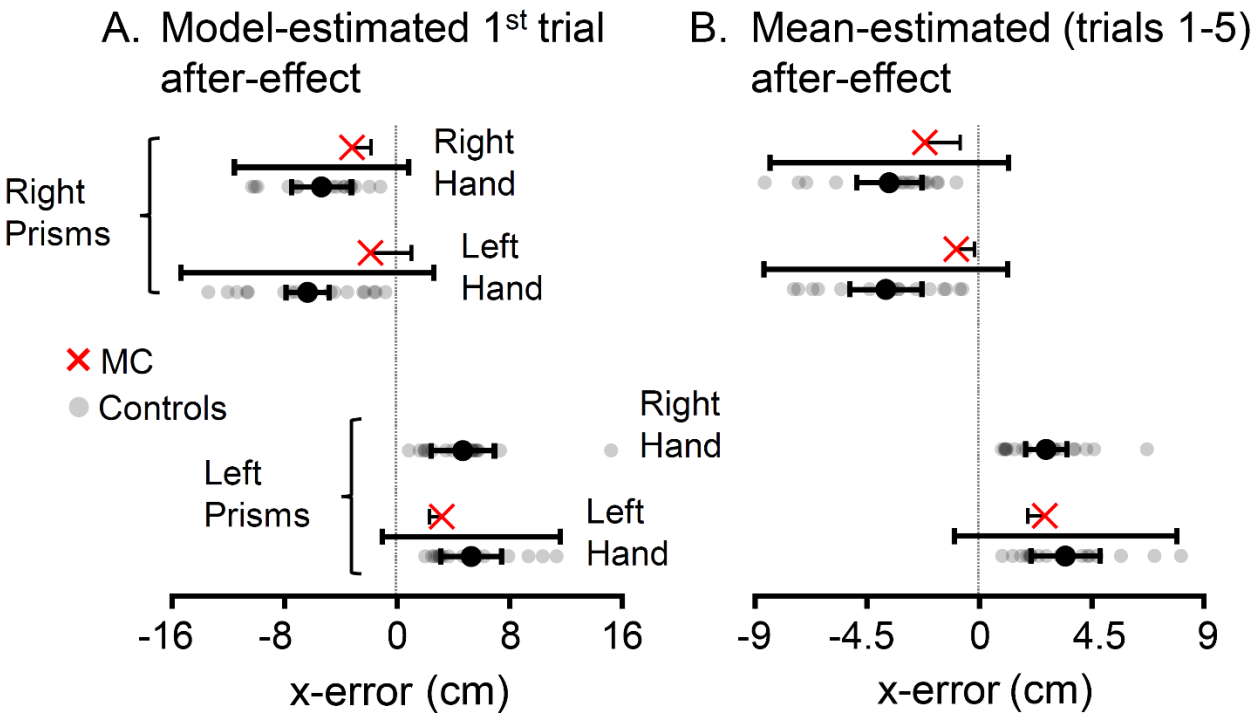
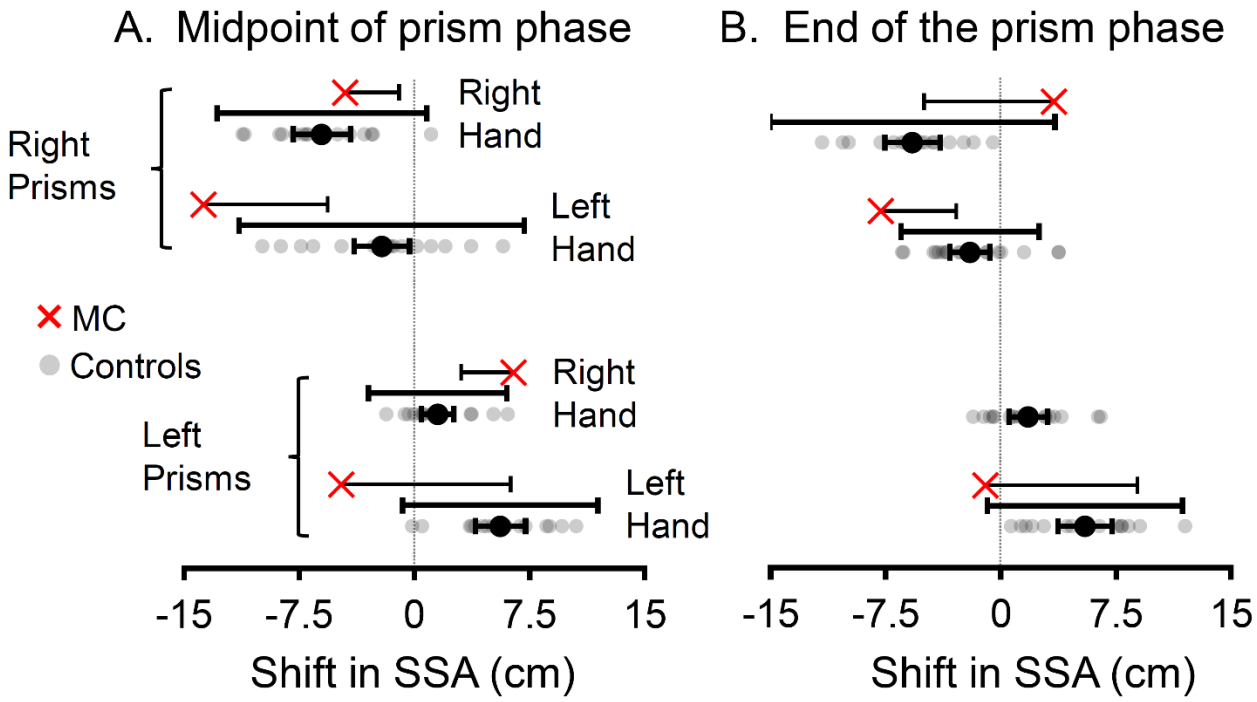

A. Model-estimated 1st trial after-effect
B. Mean-estimated (trials 1-5) after-effect
Right Prisms
Left Prisms
Right Hand
Left Hand
MC
Controls
-16
-8
0
8
16
-9
-4.5
0
4.5
9
x-error (cm)
x-error (cm)

Figure 8.


A. Midpoint of prism phase
B. End of the prism phase
Right Prisms
Right Hand
Left Hand
MC
Controls
Left Prisms
Right Hand
Left Hand
-15
-7.5
0
7.5
15
Shift in SSA (cm)
-15
-7.5
0
7.5
15
Shift in SSA (cm)