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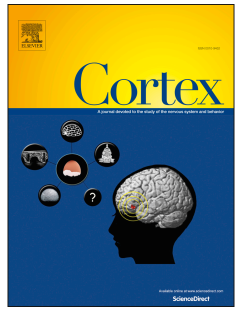

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The effect of prism adaptation on state estimates of eye position in the orbit

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Abstract

Prism adaptation (PA) after-effects are assessed using tests that measure changes in sensorimotor systems. After-effects on pointing without feedback to a visual target (open loop pointing – OLP) are traditionally described as being larger than those measured by straight ahead pointing (SAP) with eyes closed, and the difference between them is attributed to a shift in visual localisation. However, neither differences between OLP and SAP, nor shifts in perceptual judgement of visual straight ahead (VSA), are consistently reported. Moreover, since very few studies have directly recorded direction of gaze, an effect of PA on the state estimate of gaze direction has not been reliably documented. The current research aimed to isolate the effects of PA on state estimates of eye position. We measured sensorimotor after-effects through common (OLP, SAP, and VSA) measures, and also recorded eye position and additional after-effect measures to interrogate changes to the oculomotor system and how these might relate to other measures of sensorimotor change. To ascertain if PA's effects on estimates of eye position could be attributed to eye muscle potentiation, we compared the effects of PA to sustained gaze deviation without adaptation. PA induced no effect on visual straight-ahead and no change in direction of gaze, when measured while positioning a target, looking straight ahead in the dark, or looking toward the passively positioned and occluded unexposed hand. We also found that after-effects measured by SAP with the eyes open were larger than SAP with the eyes closed and equal to those observed with OLP. The findings challenge the concept that total adaptation after-effect is a direct sum of arm proprioceptive and visual after-effects as conventionally measured, and suggest that the oculomotor system is altered by prism adaptation only in interaction with an arm motor command when vision is available.

Highlights

- No evidence of a shift of visual straight-ahead or of gaze direction following prism adaptation.
- Active arm movement under the availability of vision produced largest after-effect.
- Findings challenge the concept of linear additivity of arm proprioceptive and visual after-effects of prism adaptation.

Keywords: prism adaptation; visual shift; proprioception; eye position

Declaration of interest: None

1. Introduction

Pointing toward a visual target optically displaced by refracting prisms results in aiming errors that create a conflict between the signals received from the arm and the eye and thus, a discrepancy between predicted and expected sensory feedback. Prism adaptation is the process that restores harmony between motor, proprioceptive and visual systems to provide coherent behaviour and experience. This mostly unconscious process includes a re-weighting of the reliability of the visual and proprioceptive sensory signals; a change in the relationship, in particular the spatial coding, between the sensory signals involved; and, given this new relationship, a change in motor commands to the relevant effectors (eye and arm).

Over the last two decades, prism adaptation has been investigated for its ability to reduce hemispatial neglect in stroke patients (e.g., Chen, Goedert, Priyanka, Foundas, & Barrett, 2014; Nijboer, McIntosh, Nys, Dijkerman, & Milner, 2008; Rode, Rossetti, & Boisson, 2001; Rossetti et al., 1998; Saevarsson, Kristjánsson, Hildebrandt, & Halsband, 2009; Striemer & Danckert, 2010), and to induce neglect-like changes in healthy controls (e.g., Bultitude & Woods, 2010; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Loftus, Vijayakumar, & Nicholls, 2009; Michel et al., 2003). The change that takes place in the relationship between the eye and the arm - the sensorimotor adaptation - appears essential for bringing about such higher-order cognitive, and potential therapeutic, after-effects of prism adaptation (PA) (Serino, Bonifazi, Pierfederici, & Làdavas, 2007). Arm sensorimotor changes are most frequently used to measure whether adaptation has occurred, and the changes to visual signals as a result of prism exposure have been less studied. However, there is evidence that changes to oculomotor function could underlie reduction in neglect symptoms seen after PA. Therefore, understanding the role of oculomotor function in PA could lead to a better understanding of its therapeutic effects (Angeli, Meneghello, Mattioli, & Làdavas, 2004; Serino, Angeli, Frassinetti, & Làdavas, 2006). The goal of the current study was to improve our understanding of oculomotor changes during prism adaptation. In particular, we aimed to understand whether state estimates of eye position in the orbit are recalibrated by prism adaptation, and whether post-adaptation shifts in the localisation of visual targets might be attributable to a recalibration of the state estimate in gaze direction.

Prism adaptation after-effects are usually assessed using one or more of three tests before and after exposure: visual straight-ahead (VSA) judgments, straight-ahead pointing (SAP), and open loop pointing (OLP) (for a review see, Redding, Rossetti, & Wallace, 2005). VSA involves verbally indicating visual subjective straight-ahead, usually by saying when a laterally moving light or target crosses the point that is directly in front of the body midline. The VSA after-effect (i.e., a shift in the perceived location of a visual target and, by inference, a shift in perceived 'straight-ahead' of the visual scene) is in the *same* direction of the prismatic displacement. SAP involves actively pointing the adapting arm with eyes closed to the point in space that is subjectively in front of the body midline. The felt position, or proprioception, of the adapting arm shifts in the *same* direction as the prismatic displacement (Craske, 1966; Putterman, Robert, & Bregman, 2013; Wallach & Huntington, 1973; Welch, 1969). SAP errors predominantly demonstrate a motor command that reflects the new signal of arm proprioception and are therefore in the direction *opposite* the prismatic displacement. OLP involves pointing with the unseen hand to visual targets and is conventionally construed to reflect the total after-effect (limb proprioception changes, visual system changes, and any motor adaptation). Note that open loop in the OLP task refers only to the lack of visual feedback of the pointing hand; in healthy participants arm proprioceptive feedback is available. Like SAP after-effects, OLP after-effects are in the direction *opposite* the prismatic displacement. The idea that OLP represents the combined PA after-effect is reflected in the concept of linear additivity of the sensorimotor after-effects – that is, that OLP shift is equal to the SAP shift minus the (oppositely signed) VSA shift (OLP = SAP – VSA) (Redding et al., 2005).

There is little understanding of the mechanisms underlying the VSA after-effect. Redding and Wallace, notable authorities in the sensorimotor aspects of prism adaptation, explained that the change in visual perception (i.e., the VSA after-effect) was likely due to a realignment of "retinal local sign or direction of gaze"; but these constructs were not further specified (p 303, Redding & Wallace, 2004) (see also: Redding & Wallace, 1987, 1988, 1993, 1998, 2000, 2001). On a physiological level a shift in the localization of a visual target after PA could be understood as a recalibration in the state estimate of eye position in the orbit. The location of a visual signal can be inferred by integration of information about gaze direction with information about the locus on the retina stimulated by the visual signal. For example, when looking straight ahead (with eyes centred in the orbit), a stimulus projected onto the fovea is perceived as being located straight ahead of body midline. If a perturbation causes an erroneous computation of the state estimate of eye position in the orbit, such that an eye centred in the orbit is signalled as being deviated, then a visual target projected onto the fovea will be perceived as eccentric to body midline.

Two sources of extra-retinal information influence state estimation of eye position in the orbit: the efference copy of oculomotor commands that updates the state estimate of gaze direction after each saccade, and that predicts sensory reafference resulting from the saccade; and sensory input from proprioceptors in extraocular muscles that encode the length of each extraocular muscle. Since proprioceptive input is only available after a delay following completion of the saccade, corollary discharge signals are generally considered to dominate for regulation of on-going action (Lewis, Zee, Hayman, & Tamargo, 2001; but see Weir, Knox, & Dutton, 2000). Wang, Zhang, Cohen, & Goldberg (2007) suggested that the main function of ocular proprioception is long-term calibration of the eye position state estimation that is derived from efference copy. It has been shown that eye muscle proprioceptive signals are used to recalibrate the state estimate to correct accumulating errors provided by corollary discharge signals over time (Poletti, Burr, & Rucci, 2013), and are relied upon only when there is conflict between state estimates derived from corollary discharge and proprioception (Balslev, Himmelbach, Karnath, Borchers, & Odoj, 2012).

Redding, Rossetti and Wallace asserted that the visual perceptual changes underlying the post-adaptation shift in VSA requires a “coordination of both retinal and oculomotor components” and that it involves a degree of eye muscle potentiation (see below) (Redding et al., 2005, p.441). In the absence of further elaboration, and knowing that limb proprioception is altered, their assertion may be interpreted as meaning that eye muscle proprioception is recalibrated by PA, and that the resultant change in the state estimation of eye position in the orbit engenders a shift in VSA. Investigators who studied eye position using repeated photography in the dark found a shift in eye position in the direction of prism displacement during the first 15 trials of PA while looking at a target judged to be straight-ahead (McLaughlin & Webster,

1967) and following 60 trials of PA while look straight-ahead in the absence of a target (Kalil & Freedman, 1966). The authors posited changes in ocular proprioception as an underlying cause of the shift in VSA judgements. Following adaptation to prisms that altered depth perception (perceived distance from body), Craske & Crawshaw (1974, 1978) observed the lateral estimation of target position to be shifted in opposite directions for each eye during monocular judgements. They concluded the shifts were due to an adaptation in registered eye position, which led to laterally shifted gaze as being perceived as straight ahead, which in turn led to shifted VSA.

Several assumptions underlying the account outlined above have been challenged. In particular, the concept of simple linear additivity has been thrown into question by studies that have reported patterns that do not fit the premise the total after-effect is made up of a combination of visual and proprioceptive after-effects (e.g., Bornschlegl et al., 2012; Facchin et al., 2018; Ferber & Murray, 2005; Fortis et al., 2013; Girardi et al., 2004). There has been a finding of a larger OLP after-effect compared to SAP after-effect following a full decay of the VSA after-effect (Hatada, Rossetti, & Miall, 2006), and observations of greater OLP after-effects compared to combined VSA and SAP after-effects (e.g., Welch, Choe, & Heinrich, 1974). Reports from studies finding no visual after-effect in healthy people have also accumulated (Bornschlegl et al., 2012; Choe & Welch, 1974; Harris, 1963; Herlihey & Rushton, 2012; Michel, Gaveau, Pozzo, & Papaxanthis, 2013; Morton & Bastian, 2004; Newport, Preston, Pearce, & Holton, 2009). The lack of observable visual after-effect in many studies alongside the pattern of deviations from linear additivity suggest that there might be an issue with how the VSA after-effect has previously been measured, or how the visuomotor change is understood.

In addition, an alternative explanation for shifts in VSA argues that adaptation *per se* does not produce recalibration of proprioception in extraocular muscles, but rather that it is the result of eye muscle potentiation (EMP). EMP is induced by sustaining a deviated gaze - a consequence of prism exposure - leading to persisting innervation of extra-ocular muscles. By this account, the VSA shift is not due to conflict between the hand and eye, nor to a change in the reliability of eye position signals, but to the continuing execution of motor commands that have accumulated (due to the sustained nature of the deviation) at the neuromuscular junction. Proponents of the eye muscle potentiation account of the VSA shift have pointed to similarities in the after-effects of sustained ocular deviation and PA (Ebenholtz & Wolfson, 1975; Paap & Ebenholtz, 1976). From this perspective, the post PA change in visual perception is not (solely) due to sensorimotor adaptation, but is partially due to the physiological side effect of sustaining a deviated gaze. Challenging this stance, a VSA shift has been found following an eye muscle potentiation but not following a prism adaptation condition (Newport et al., 2009).

The main goal of the current research was to seek evidence that adaptation produces a recalibration the state estimate of eye position in the orbit and that this recalibration induces a shift in the localization of visual signals. We measured a series of sensorimotor effects before and after participants underwent right-shifting prism adaptation (R-PA) or right-shifting eye muscle potentiation (R-EMP). The R-EMP condition was achieved by having the participant point without vision of the hand while looking through a right-shifting prism. In this way, the participants' eyes sustained the directional deviation imposed by the prismatic displacement, but adaptation did not take place because the mismatch between arm and eye signals went undetected. R-PA was achieved using identical procedures except the participants could see their adapting hand and the terminal error. We built upon the study by Newport and his co-workers (Newport et al., 2009) by increasing the number of after-effect tests (conventional and new) to interrogate changes to the oculomotor system, and how these might relate to other measures of sensorimotor change.

We used a high-resolution eye-tracker to measure eye position in the orbit in addition to perceptual measures of VSA. We used eye position measures to investigate oculomotor system changes while we used a task involving moving a bar to visual straight-ahead to interrogate visual perceptual changes – both were measured during a VSA task. We included conventional SAP and OLP tests to examine the context within which oculomotor and visual changes occur.

In addition, we developed a SAP with eyes open task (an interim step between conventional SAP and OLP), during which we measured eye position before and simultaneous to pointing straight-ahead. There are two differences between the

SAP and OLP tasks that may aid in understanding the source of the VSA after-effect: The state of the eyelid (closed versus open) and the target type (internal representation of the arm versus visual). In one trial of this new task, we captured a VSA eye position measure (looking straight ahead with no visual target) and another eye position measure while the hand and the eye were completing the same goal (movement to straight-ahead). By measuring both pointing error and eye position during this task, we aimed to probe whether the hand and eye would act in a coupled or uncoupled manner in the absence of a visual target following R-PA and R-EMP.

Finally, we included finger localisation tasks for the exposed and unexposed hands, in which participants indicated the location of each unseen passively moved arm from oculomotor information. Any R-EMP after-effects should be the same for each arm. Because there was no change in trajectory of pointing during prism exposure, no limb proprioceptive R-PA after-effects were expected for the unexposed arm; (Taub & Goldberg, 1973; Scarpina et al, 2013; Mostafa et al, 2014; but see Wallace, 2008). Therefore, any oculomotor after-effects exclusive to adaptation should be seen in the difference between errors locating the unexposed hand following R-PA and the R-EMP after-effects. (The R-PA after-effects for the exposed hand would reflect the combination of limb proprioception plus any R-EMP and oculomotor adaptive changes.)

Predictions for each task are summarised in table 1. We expected that any pointing after-effects and the passively moved exposed arm localisation would be larger in magnitude for R-PA than for R-EMP due to the involvement of a limb proprioceptive after-effect in the former and not the latter. The likely relative magnitude of eye position after-effects following R-PA compared to R-EMP was less clear to us. On one hand, the R-EMP condition exposes the eye to the full extent of sustained gaze toward the displaced visual targets for the entire exposure period, while for the R-PA condition the error feedback allows the eye the opportunity to move against the prism deviation (towards the adapting hand). This suggests that we could expect a larger R-EMP eye position after-effect compared to R-PA. On the other hand, R-PA is an adaptation condition, and the magnitude of the conventionally understood shift in eye position relative to a sustained eye deviation shift remains under-investigated.

Table 1: The after-effect task used in this study, along with the predicted and observed directions of each.

Methods Section	Task	Position Measure	Shift	Predicted after-effect direction	Observed after-effect direction
2.4.3	VSA measures	Eye & Verbal	R-PA REMP	right	no after-effect
2.4.4	SAP eyes closed	Point	R-PA	left	left
			R-EMP	No after-effect (straight ahead)	no after-effect
2.4.5	SAP eyes open, pre pointing	Eye	R-PA	Left if aligned and interacting with limb OR right if adapted but not interacting with limb	no after-effect
			R-EMP	Straight-ahead (no after-effect) if guided by limb OR right if eyes not interacting with limb	right
2.4.5	SAP eyes open	Point	R-PA	left	left
			R-EMP	Straight-ahead (no after-effect) if guided by limb OR right if limb interacting with eyes	no after-effect
2.4.5	SAP eyes open, upon pointing	Eye	R-PA	Left if aligned and interacting with limb OR right if adapted but not interacting with limb	no after-effect
			R-EMP	Straight-ahead (no after-effect) if guided by limb OR right if eyes not interacting with limb	right
2.4.6	OLP	Point	R-PA	left	left
			R-EMP	right	no after-effect
2.4.7	Finger localisation, exposed hand	Eye	R-PA R-EMP	right (R-PA > R-EMP)	right for R-PA only
		Verbal	R-PA REMP	right (R-PA > R-EMP)	right for R-PA only
2.4.7	Finger localisation, unexposed hand	Eye	R-PA R-EMP	right	right
		Verbal	R-PA R-EMP	right	right

2. Methods

In a within-subject design each participant was exposed to each condition (R-PA, R-EMP) in separate sessions a minimum of one week apart. In each session there was a sham exposure (neutral lens) and a prism exposure (either R-PA or R-EMP) task, both followed by after-effect tasks (see Table 2). Responses were captured using a touchscreen, a trackpad, verbal responses, and eye tracking. The dependent variable for each task was the error between the location indicated using these responses and the objective position of the relevant target.

2.1 Participants

Twenty-three participants were recruited from the Bangor University community based on right-handedness and normal or corrected-to-normal vision. Testing was terminated early for five participants due to problems tracking their eyes and/or recording touch due to arm length. The mean age for the remaining 18 participants was 25 years (SD = 5.2, range 20-40) and the gender mix was M/F = 6/12. Informed consent was received according to the university ethics committee guidelines. All participants were financially compensated for their time (£21 for ~3.5 hours) and received a verbal debrief.

2.2 Apparatus

All tasks took place at a desk in a dark windowless room. Participants sat in a height-adjustable computer chair. Upon the desk was a structure custom-built for accommodating the equipment necessary for administering prism adaptation and eye movement potentiation, measuring eye movements and end-point errors, and occluding the pointing arm as necessary (Figure 1).

To track the eyes during adaptation it was necessary to place a tower-mounted eye-tracker (Eyelink 1000) between the prism lens and the eyes. The lenses were placed 22cm from the eyes and 31cm from the touchscreen in a fitment that held the plane of the lenses parallel to the plane of the torso. In place of conventional prism goggles, a large square (30 x 30 cm) 40 dioptre (21.8°) Fresnel prism lens (RHK Japan Inc) was used (see Bultitude et al., 2016 for a similar method of inducing prism exposure). Given its placement between the eyes and the screen the prism created an effective shift of 13.16°. The sham “lens” (also 30 x 30 cm) was made of clear

Perspex. A forehead and chin rest kept the head stable, and side-blinkers restricted viewing to forwards/through the lens with a viewing window of 27 x 20 cm. A custom-designed mounting frame (130 x 60 x 35 cm) accommodated the set-up, while also allowing unrestricted access to and movement of the arms underneath the frame. The frame also held a retractable piece of matt black reinforced cardboard that could be used to occlude the arm from view. The arm occluder attached to the top of the frame, and spanned the horizontal distance between the participant and the touchscreen, or 4 cm short of the touchscreen upon retraction. The last piece of custom-built equipment was a removable board upon which the participant could rest their hand underneath the rest of the structure. This Perspex-covered black painted board (55 cm wide x 41 cm deep) could be attached to the frame in front of the screen and a height-adjustable support (max height 25 cm) was placed underneath it. A similar sized piece of cardboard was placed on top of the board. The low-friction surfaces of both materials facilitated passive movement of the participants' hands by the experimenter.

Stimuli were presented on, and some task responses recorded from, a flat-screen landscape backlit LED-LCD touchscreen monitor (HannsG model HT271HPB, 1920 x 1080 resolution, 59 Hz). This was positioned at a distance of 53 cm from the edge of the table. An offset matt black frame covered some of the display leaving 44.5 x 24.5 cm visible while also overhanging the edges of the monitor by 23 cm to the right and 23.5 cm to the left; a 59 x 8 cm portion was within touch but out of sight below the arm occluder. The offset of the LCD screen and the matt frame were designed to minimise participants' use of contextual spatial information while encouraging judgements based on participant body position.

All tasks were programmed and executed, and behavioural responses were recorded, using Matlab (R2014a). The software ran on a Windows 7 Stone PC-1210 with a Windows 64-bit operating system. All visual stimuli were white (R = 255 G= 255 B = 255) presented on a black background (R = 0 G = 0 B = 0). All auditory stimuli were 0.5 s tonal beeps (1Khz frequency sampled at 8Khz) played from the touchscreen's in-built speakers. A trackpad (Logitech T650, 13.5 x 12.8 cm), strapped to participant's chest, responded to touch commands to either initiate a trial or record a response depending on the task. A dim backlit keyboard, (Trust 17365-03), was used by experimenter to record verbal responses.

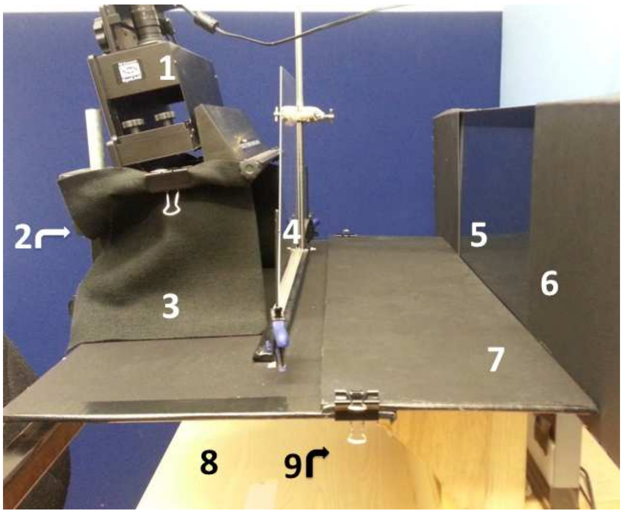

Figure 1: Apparatus side view.
1) tower-mounted eye-tracker
2) forehead and chin rest
3) side blinkers
4) lens (prism/Perspex)
5) touchscreen (turned off, visible part)
6) extender frame
7) retractable arm occluder
8) space for arm movements
9) touchscreen (hidden part)

2.3 General Procedure

Task procedure is displayed in table 2. We deemed it unfeasible to effectively counterbalance six after-effect tasks. Instead we decided to include top-ups of the sham/exposure task after every two after-effect tasks to minimise de-adaptation following exposure. Similar 'top-up' adaptation sets have been used previously (Bultitude, Downing, & Rafal, 2013; Bultitude, List, & Davies, 2013; Bultitude, Van der Stigchel, & Nijboer, 2013; Schindler et al., 2009). We included a 10 min break between the baseline and exposure testing. Equipment adjustments took less than 30 s per task, except for the finger localisation task, which took approximately 4 minutes in its first instance per condition. Participants remained in place at the chinrest with eyes closed during set-ups and between tasks.

Participants were advised not to "over-think" any tasks to encourage them to indicate their initial perceptual judgements rather than calculated or reasoned estimates for the different tasks. Instructions for the SAP and VSA tasks were designed to encourage judgements arising from the participant's own body rather than peri-personal space. Specifically, participants were instructed that SAP required pointing straight ahead of the line formed between the nose and belly-button, and that VSA was letting the eyes rest in a natural forward position. To avoid spatial decisions being influenced by room layout participants were led into the testing room with eyes closed and kept their eyes closed until the equipment was adjusted to achieve a comfortable seating position.

2.4 Tasks (stimuli & description)

The list of tasks is set out in order of their completion in table 2.

Table 2: The order of experimental tasks. Sham tasks used the Perspex “lens”; exposure tasks used the Fresnel lens. The EMP session was completed in the week prior to the PA session.

Methods section	Task	No. of trials
2.4.2	Sham PA or EMP	96 (neutral lens)
2.4.3	Visual Straight Ahead	24
2.4.4	Straight Ahead Pointing (eyes closed)	8
2.4.2	Sham Top-Up	30
2.4.5	Straight Ahead Pointing (eyes open)	8
2.4.6	Open Loop Pointing	36
2.4.2	Sham Top-Up	30
2.4.7	Finger Localisation (R hand)	8
2.4.7	Finger Localisation (L hand)	8
	Break	10 minutes
2.4.2	Real PA or EMP	96 (prism lens)
	After-effect tests are repeated, but with the sham lens replaced by the prism lens during the exposure and top-ups	

2.4.1 Calibration.

A 5-point eye-tracker calibration procedure preceded each task except SAP as measured with eyes closed. Following piloting, the position of the calibration targets on the vertical plane varied according to the area of visual focus of the subsequent task (above centre prior to the VSA task, below centre prior to the finger localisation tasks, and centred on the visible display for all other tasks) to increase calibration accuracy. Finally, the calibration annuli positions were horizontally jittered to ensure they were spatially non-informative.

2.4.2 The sham and exposure tasks.

The baseline sensorimotor tasks were preceded by sham exposure during which a Perspex panel was used as the "lens". In the exposure tasks the Fresnel prism was used to produce prism adaptation or eye muscle potentiation in the R-PA and R-EMP conditions respectively.

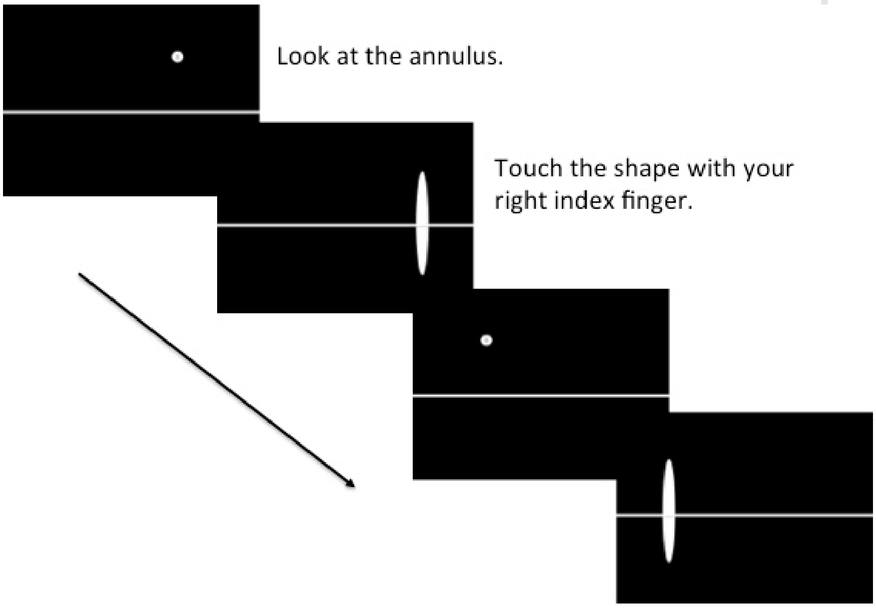

Figure 2: Two trials from the sham/exposure task. The horizontal line represents the level of the arm occluder. In the R-EMP condition (and its associated sham block), the occluder abutted the touchscreen thus hiding the pointing arm and preventing visual feedback. In the R-PA condition (and its associated sham block), there was a 3 cm gap between the occluder and the touchscreen allowing the top of the finger to be seen as it neared the screen (terminal pointing).

See figure 2 for a schematic of the task and participant instructions. The participant used their right hand for these tasks. A fixation annulus (0.6° x 0.6° with an inner hole of 0.2° x 0.2°) appeared on the screen in pseudo-random locations. Upon the participant swiping the trackpad the annulus disappeared and in a nearby location (within 5.4° s to the left or right) an elongated oval target (1° pixels wide x

10° pixels high) appeared on screen. Upon participants touching the on-screen target, it disappeared and was replaced by a new fixation annulus. There were 96 trials for the main exposure tasks and 30 in each of the top-ups. The target appeared an equal number of times in three positions: centre screen, 10.7° to left and 10.7° to right of centre (pseudorandom order). The use of multiple target locations presented in pseudorandom order aimed to limit any motor bias that can develop, independently of a motor response to proprioceptive adaptation, when pointing is predictable and repetitive.

All the stimuli during the exposure tasks (and their related calibrations) were displaced to the left by 6.7° relative to their location during sham exposure. This step was taken to ensure that pointing errors (and after-effects) caused by the displacement would fall within the boundaries of the touchscreen.

A chinrest, forehead rest, and blinkers were use throughout the experiment to facilitate eye-tracking and minimised any neck proprioceptive after-effect.

The response was recorded as the first touch on the touchscreen. For R-PA exposure it was expected that the initial rightward pointing errors would decrease toward baseline with continuing exposure. For the R-EMP exposure it was expected that rightward pointing errors would be stable and remain uncorrected throughout the exposure period.

2.4.3 Visual straight ahead (VSA).

The conventional VSA task was amended to facilitate eye-tracking, it therefore precluded a verbal response that would have perturbed the preceding calibration. The different elements of this task aimed to measure changes in two measures relative to sham exposure. First, perceptual VSA was measured by asking participants to stop a bar with the unseen non-adapting hand when the bar was judged to be straight ahead. Second, the oculomotor VSA was measured as the position of the eye as they gazed to what they perceived as straight ahead (both before the bar appeared on screen and as the bar was positioned straight-ahead).

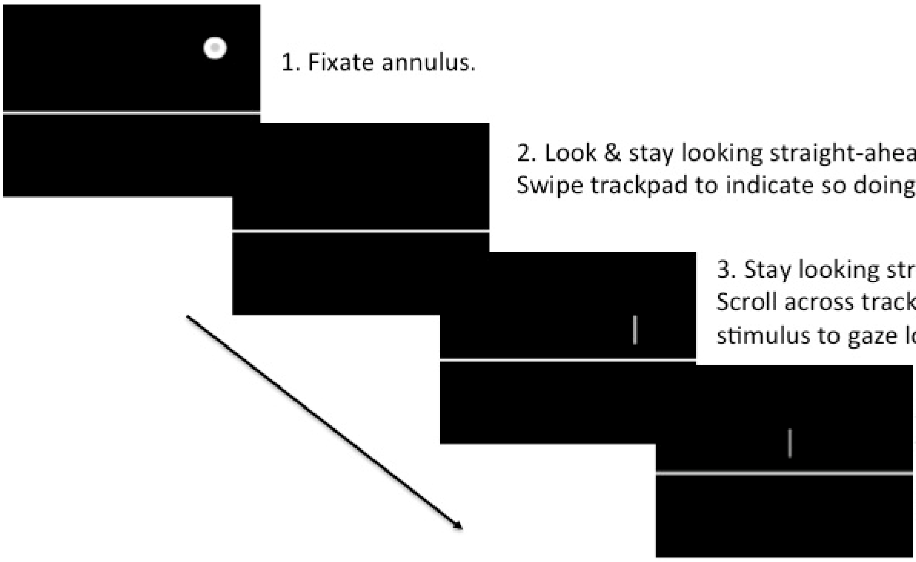

Figure 3: One trial from the VSA task. The horizontal line represents the level of the arm occluder on the screen.

See figure 3 for a schematic of the task and participant instructions. A fixation annulus appeared. Verification of accurate fixation (i.e., the representation of the eye overlapped the position of the stimulus) was assessed on the experimenter’s monitor. Upon verification the annulus immediately disappeared, the participant looked straight-ahead and swiped the chest trackpad using their non-adapting left index finger. A vertical stimulus (.34° wide, 4° high) appeared at the same location as the original annulus. The participant stayed looking straight-ahead and scrolled across the trackpad to bring the stimulus to meet their gaze. They knocked on the table to indicate their final response. There were 24 trials split equally between a starting point that varied, in equal increments of 0.275°, between 9.4° and 12.7° either on the left or right of the centre of the screen and presented in a pseudorandom order.

Eye positions selected for analysis of oculomotor VSA were the last fixation after the disappearance of the annulus/before the appearance of the bar stimuli and the last fixation with the bar in position. If no fixation was recorded during an element of a trial, the endpoint of the last saccade was taken. The perceptual VSA was recorded as the final position of the bar on the touchscreen.

2.4.4 Straight ahead pointing (SAP) – eyes closed.

With eyes closed, participants were instructed to hold their right index finger in front of the trackpad and keep their elbow elevated. Following a beep, participants reached and touched the touchscreen at the point straight ahead of their body midlines, and return their finger to swipe the trackpad to end the trial. There were eight trials. The beep was presented at jittered intervals of 2-5 s to help minimise any rote responding. The response was recorded as the first touch on the touchscreen.

2.4.5 Straight ahead pointing (SAP) – eyes open.

See figure 4 for a schematic of the task and participant instructions. With eyes open, participants were instructed to hold their right index finger in front of the trackpad and keep their elbow elevated. A fixation annulus appeared, and the experimenter pressed a button once the participant had fixated. The annulus immediately disappeared and the participant looked straight-ahead. A second fixation annulus appeared, and the experimenter pressed a button once the participant had fixated. This second annulus immediately disappeared and the participant simultaneously looked, reached and touched the touchscreen at the point straight ahead of their body midline. They returned their finger to swipe the trackpad to end the trial.

Across the trials the annuli appeared in locations split equally between 9.5° and 12.5° to the left and right of screen centre, within trial locations were jittered. There were eight trials.

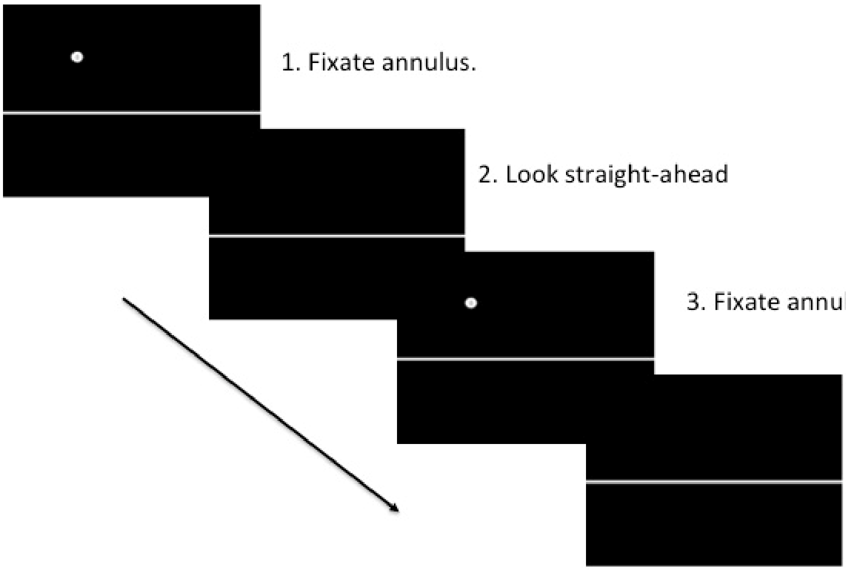

Figure 4: One trial from the straight-ahead pointing with eyes open task. The horizontal line represents where the arm occluder touched the screen.

The pre-SAP eye position measure was selected as the last fixation after the disappearance of the first annulus, made without any simultaneous SAP arm movement from the participant. The upon-SAP eye-position measure was selected as the last fixation after the disappearance of the second annulus, measured at approximately the same time as the participant made their SAP movement. These two straight-ahead measures, in the absence of a visual target, are differentiated by respective absence/presence of an arm movement – states which may influence the behavioural response. The pointing response was recorded as the first position touched on the touchscreen.

2.4.6 Open loop pointing (OLP).

See figure 5 for a schematic of the task and participant instructions. The participant began with the finger of their right hand in front of the trackpad. A fixation annulus appeared, either 5.5° to left or right of screen centre, and the experimenter pressed a button once the participant had fixated. The annulus immediately disappeared and a target (.34° wide, 13.4º visible height) appeared on the same side of the screen as the annulus had been. The participant pointed, as accurately as possible, with the index finger of their occluded exposed (right) hand at the target and returned their finger to swipe the chest trackpad to end the trial. There were 36 trials. Targets were presented across the width of the screen at 36 individual locations, separated by equal increments, from 10.7° left of to 10.7° of right of centre, in pseudo-random order. Half were presented left of screen centre and the remaining in mirror positions to the right of centre. The pointing response was recorded as the position touched on the touchscreen.

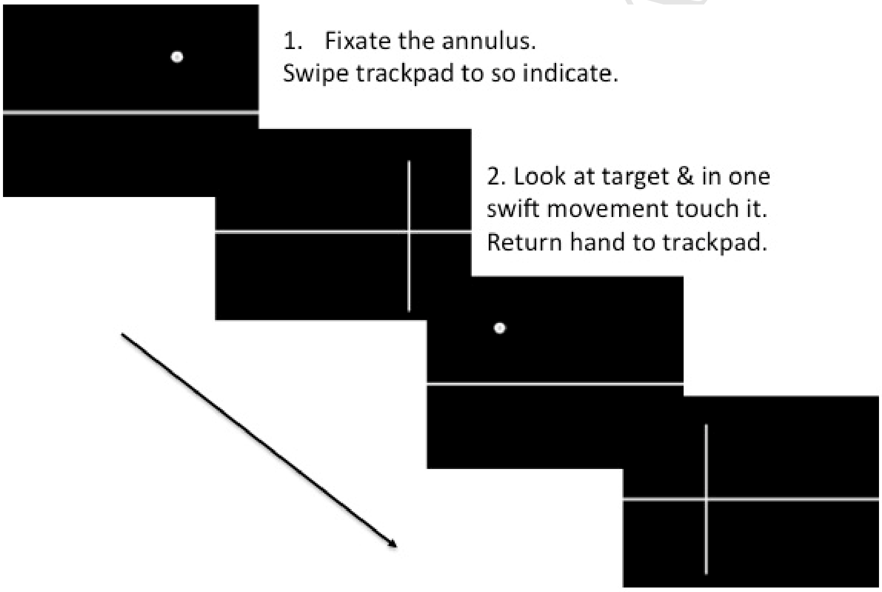

Figure 5: Two trials from the open loop pointing task. The horizontal line represents where the arm occluder touched the screen.

2.4.7 Finger localisation.

See figure 6 for a schematic of the task and participant instructions. This task was run first for the right (exposed) hand and then the unexposed left hand with eye tracking calibrations before each. The experimenter moved the participant’s unseen hand (palm down) into an unseen position and then lightly touched the participant's middle finger as a cue that the trial had begun. A fixation annulus appeared, and the experimenter pressed a button once the participant had fixated. The annulus immediately disappeared and the participant looked at the point on the blank screen that they judged to be vertically above with their cued finger. A fixation annulus appeared, and the experimenter pressed a button once the participant had fixated. The annulus immediately disappeared and a blank scale appeared. The participant looked at the point on the scale that they judged to be vertically above with their cued finger. Scale labels appeared, the participant looked at the appropriate label and then named it aloud. The trial ended when the experimenter keyed in the response.

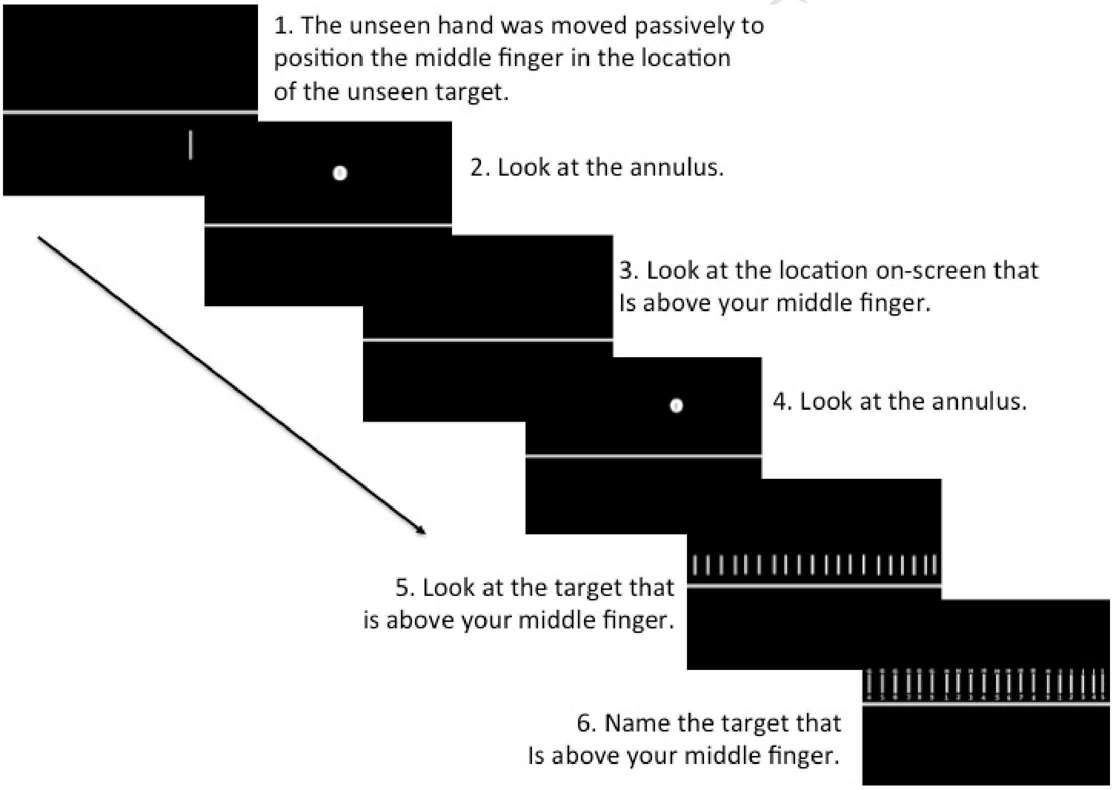

Figure 6: One trial from the finger location task. The horizontal line represents where the arm occluder touched the screen. The last screen shows scale identifiers above and below each scale marking.

The horizontal scale consisted of lines distributed across the width of the screen, 0.5° apart. After 4 s labels appeared on the scale with letters on its upper part and corresponding one digit numbers on the lower part, e.g., B7 (these alphanumeric labels were used because the alphabet alone was too short for the screen and using digits alone would have created variability in visual crowding across the screen). Letter allocation varied per trial to minimise any use of strategy and to encourage the participant to provide body-centred responses. The experimenter entered the verbal response by keyboard. Eight trials were performed with pre-determined positions: four positions each for left and right of body midline (in pseudo-randomized order).

Eye position measurements were taken at blank screen: the last fixation following the disappearance of the annulus; the un-numbered scale: the last fixation; and numbered-scale: the last fixation. These task steps (3, 5 and 6 respectively) varied in the amount of visuospatial information available to the participant. The perceptual response was key-press recorded by the experimenter.

2.5 Analysis

For each task, the raw error between the objective target and the participant's response was captured in pixels, and converted to degrees of visual angle. Analyses were conducted using repeated measures ANOVAs, with the independent variables of Time (post-sham, post-shift) and Shift (R-EMP, R-PA). The dependent variable was the error. Negative values denote leftward, and positive values denote rightward after-effects. Analyses were completed using *R* basic (R Core Team, 2016) and additional packages (Grosjean, Ibanez, & Etienne, 2014; Hothorn, Bretz, & Westfall, 2008; Wickham, 2009; Wickham, Francois, Henry, & Müller, 2017).

3. Results

An overview of the results can be found in table 1. Significant leftward pointing after-effects were found following R-PA (SAP as measured with eyes closed, SAP as measured with eyes open, and OLP). There were no significant point after-effects in the R-EMP condition. Significant rightward eye position in orbit after-effects were found in one task following R-EMP (SAP as measured with eyes open), but none were found following R-PA. Neither condition resulted in a shift in visual perception of subjective straight-ahead. A significant rightward shift in visual localisation of the passively moved arm was evident in the exposed hand following R-PA, but no other significant after-effects were found in the finger location tasks for either condition.

3.1 Errors during exposure.

Pointing errors during the sham and exposure conditions are illustrated in Figure 7. As expected, rightward pointing errors declined rapidly (from 12° in the first pointing trial to 4° by trial 15) during the initial R-PA exposure. Errors did not return to baseline by the end of the first exposure period compared to sham ($p < .001$) (bin 32 in figure 7) but they did by the end of each of the two top-up periods ($p \geq .089$, bins 42 and 52 in figure 7). These direct errors suggest that participants might not have been *fully* adapted when they undertook the first two after-effect tasks but were fully adapted for the later tasks. As predicted, the rightward pointing errors during R-EMP remained constant throughout all three exposure-periods (figure 7).

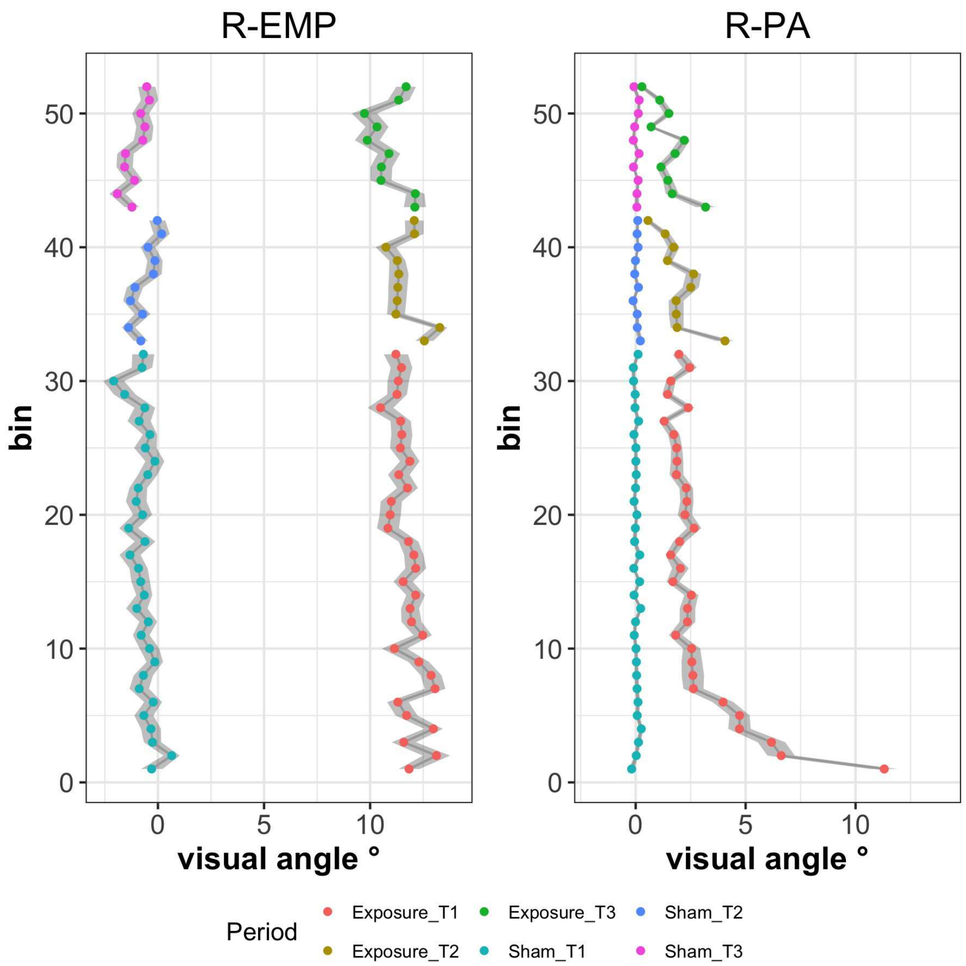

Figure 7: Mean pointing error per Shift during the sham and exposure periods based on observed data. Each data point represents the mean of three trials (or 1 bin). There were 32 bins in the period T1 and 10 each in top-up periods T2 and T3. The ribbon effect = SE. Positive values = rightward error.

3.2 After-effects

Analysis of eye position and perception for visual straight ahead

As show in figures 8 (oculomotor VSA) and 9 (perceptual VSA), contrary to predictions of a rightward after-effect, there were no changes in any of the three VSA after-effect measures following either R-PA or R-EMP exposure. This suggests that, following 96 exposure trials, neither manipulation had any effect on the state estimation of eye position in the orbit. There were no main effects of Time or Shift and no interaction in the analyses of all three measures for the VSA task (Fs $\leq$ 2.77, ps$\geq$.099).

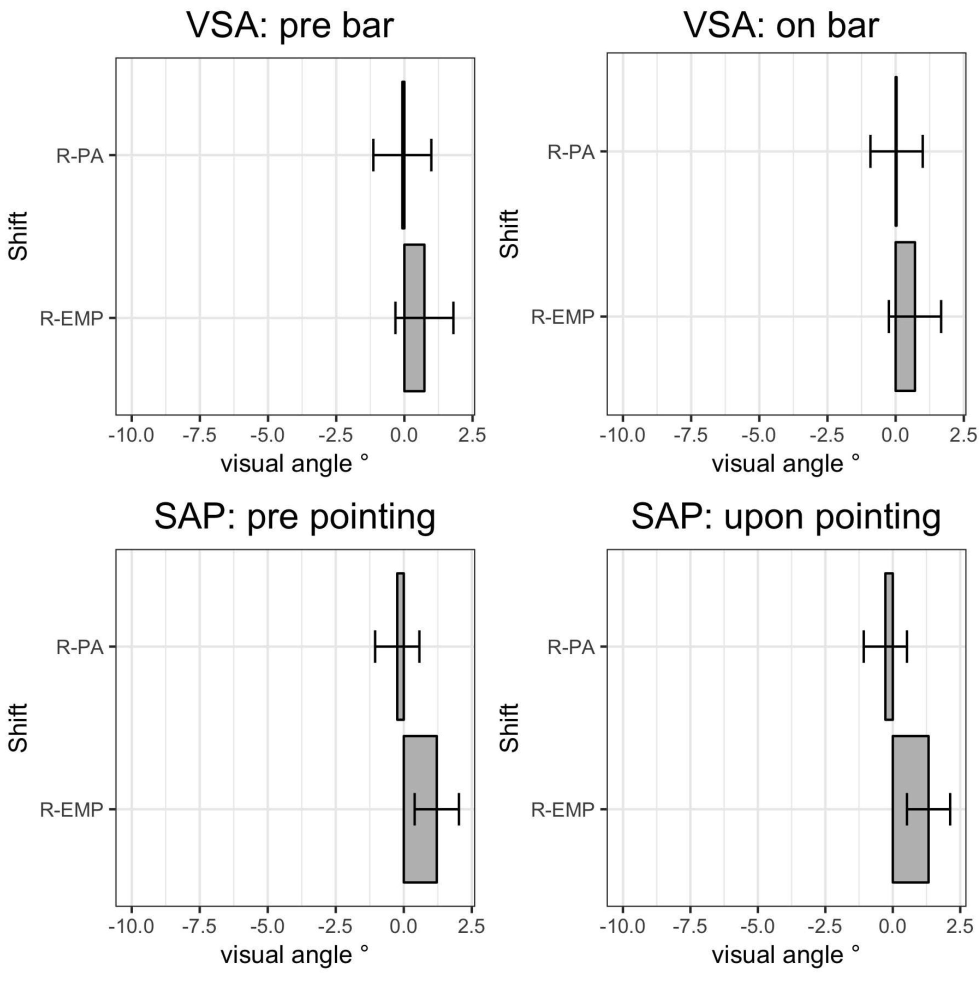

Figure 8: Mean after-effects in degrees of visual angle. Top row: prior to (left) and upon (right) positioning a bar to VSA with the unseen unexposed hand. Bottom row: prior to (left) and upon (left) SAP with the unseen exposed hand. Error bars are 95% confidence intervals. Positive values = rightward after-effect.

Analysis of pointing errors during straight-ahead pointing – eyes closed.

There was a main effect of Time (F(1, 17) = 29.6, p < .001, η_G^2 = .056), no main effect of Shift (p = .094), and a significant effect of their interaction (F(1, 17) = 21.8, p < .001, η_G^2 = .122), see figure 9. Consistent with predictions, there was a significant leftward pointing after-effect in the R-PA condition in the SAP-eyes closed task, (M = -4.53, 95% CI [-3.15, -5.90], t(26.8) = -6.74, p < .001, r^2 = .793). Also, as predicted, there was no SAP after-effect following R-EMP (p = .175).

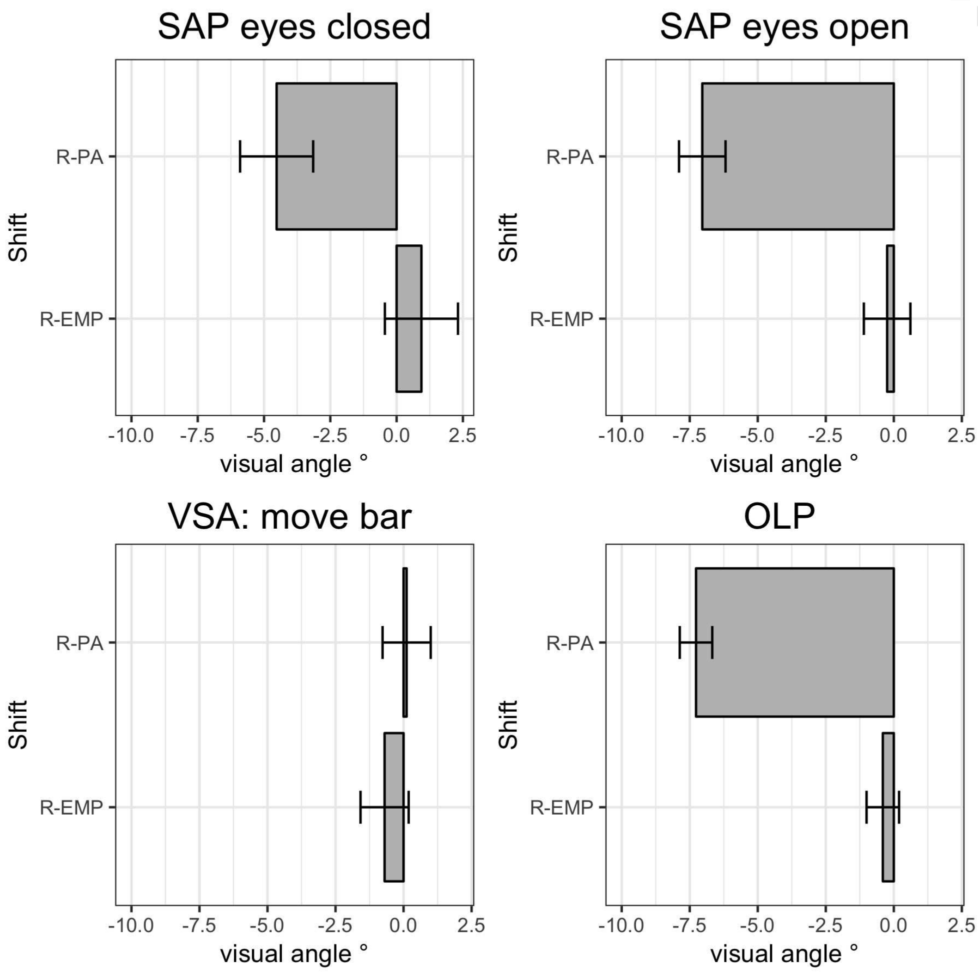

Figure 9: Mean perceptual and pointing after-effects in degrees of visual angle. Top row: SAP eyes closed pointing (left) and SAP eyes open pointing (right) with the unseen exposed hand. Bottom row: perceptual VSA (left), OLP pointing with unseen exposed hand (right). Error bars are 95% confidence intervals. Negative values = leftward after-effect.

Analysis of pointing and eye position during SAP pointing, eyes open

In the analysis of eye position and pointing after-effects for the SAP task with eyes open there were significant interactions between Time and Shift in all three elements of the task. ***Element 1: Look straight-ahead prior to SAP (Eye position).*** Time ($F(1, 17) = 5.55$, $p = .031$, $\eta_G^2 = .032$), Shift ($p = .557$), Interaction ($F(1, 17) = 4.58$, $p = .047$, $\eta_G^2 = .068$). ***Element 2: Point straight-ahead.*** Time ($F(1, 17) = 219$, $p < .001$, $\eta_G^2 = .448$), Shift ($F(1, 17) = 16.7$, $p < .001$, $\eta_G^2 = .273$), Interaction ($F(1, 17) = 100$, $p < .001$, $\eta_G^2 = .413$). ***Element 3: Look and point straight (Eye position).*** Time ($F(1, 17) = 7.28$, $p = .015$, $\eta_G^2 = .032$), Shift ($p = .188$), Interaction ($F(1, 17) = 5.60$, $p = .030$, $\eta_G^2 = .072$).

As illustrated in figure 8, in contrast with predictions of a rightward after-effect, following R-PA there was no change in either of the two eye-position measures taken during the SAP eyes open task – eye-position remained in the straight-ahead position in the orbit (element 1: $p = .551$; element 3: $p = .486$). Thus, these eye-position measures provided no evidence supportive of a change in ocular spatial coding.

Consistent with the emergence of eye muscle potentiation, following the R-EMP condition there was a significant rightward after-effect of both eye position measures, figure 8, (element 1: M = 1.21, 95% CI [0.399, 2.03], $t(28.1) = 3.05$, $p = .005$, $r^2 = .499$; element 3: M = 1.33, 95% CI [0.525, 2.13], $t(27.1) = 3.39$, $p = .002$, $r^2 = .546$). There was no change in straight-ahead pointing (ps $\geq .05$). These R-EMP results are consistent with a lack of interaction between the ocular and limb systems. As depicted in figure 9, there was a significant leftward after-effect in pointing following R-PA (M = -7.04, 95% CI [-7.89, -6.18], $t(31) = -16.79$, $p < .001$, $r^2 = .949$) but no change following R-EMP ($p = .563$).

Analysis of pointing errors for OLP (pointing to visual target, hand unseen).

In the analysis of pointing errors for the OLP task there was a significant effects of Time ($F(1, 17) = 285$, $p < .001$, $\eta_G^2 = .466$) and of Shift ($F(1, 17) = 15.8$, $p < .001$, $\eta_G^2 = .282$), and their interaction, ($F(1, 17) = 341$, $p < .001$, $\eta_G^2 = .412$), illustrated in figure 9. Concordant with predictions, there was a significant leftward pointing after-effect in the R-PA condition (M = -7.27, 95% CI [-7.87, -6.67], $t(32.7) = 24.8$, $p < .001$, $r^2 = .974$). This active task is understood to reflect the combined adaptive responses of limb and ocular proprioception (i.e., linear additivity, OLP = SAP – VSA). Against predictions that R-EMP would result in a rightward after-effect (albeit smaller in magnitude than that observed following R-PA), there was no error change following R-EMP (M = -0.404, 95% CI [-1.00, 0.193], $t(32.7) = 1.38$, $p = .178$, $r^2 = .234$).

Comparisons across R-PA pointing tasks after-effects.

No VSA after-effect was found following R-PA, yet OLP was numerically greater than SAP measured while the eyes were closed. Furthermore, figure 10 appears to show that both SAP, measured while the eyes were eyes open, and OLP prompted a larger after-effect than SAP measured while the eyes were closed. To investigate these differences, the mean pointing responses of the SAP eyes closed, SAP eyes open, and OLP tasks after R-PA were submitted to a repeated-measure ANOVA with the factors Time (post-sham, post R-PA) and Task (SAP eyes closed, SAP eyes open, OLP). There was a main effect of Time ($F(1, 17) = 295$, $p<.001$, $\eta_G^2 = .628$) reflecting the leftward pointing after-effect brought about by all tasks. The Greenhouse-Geisser corrected main effect of Task, ($F(1.31, 22.2) = 3.29$, $p= .07$, $\eta_G^2 = .061$), was not significant – all tasks induced a leftward pointing after-effect. The Time by Task interaction was significant, ($F(1.50, 25.5) = 13.5$, $p<.001$, $\eta_G^2 = .062$). Follow-up Bonferroni-adjusted Tukey comparisons revealed that there was no difference between the post-errors of OLP and SAP measured with the eyes open ($p = .99$). However, the post-errors for OLP were significantly larger than those for SAP measured with the eyes closed ($p < .001$). Also, the post-errors for SAP measured with the eyes open were significantly larger than those for SAP measured with the eyes closed ($p = .013$). There were no differences across the various combinations of the tasks pre exposure (*p*s > .99).

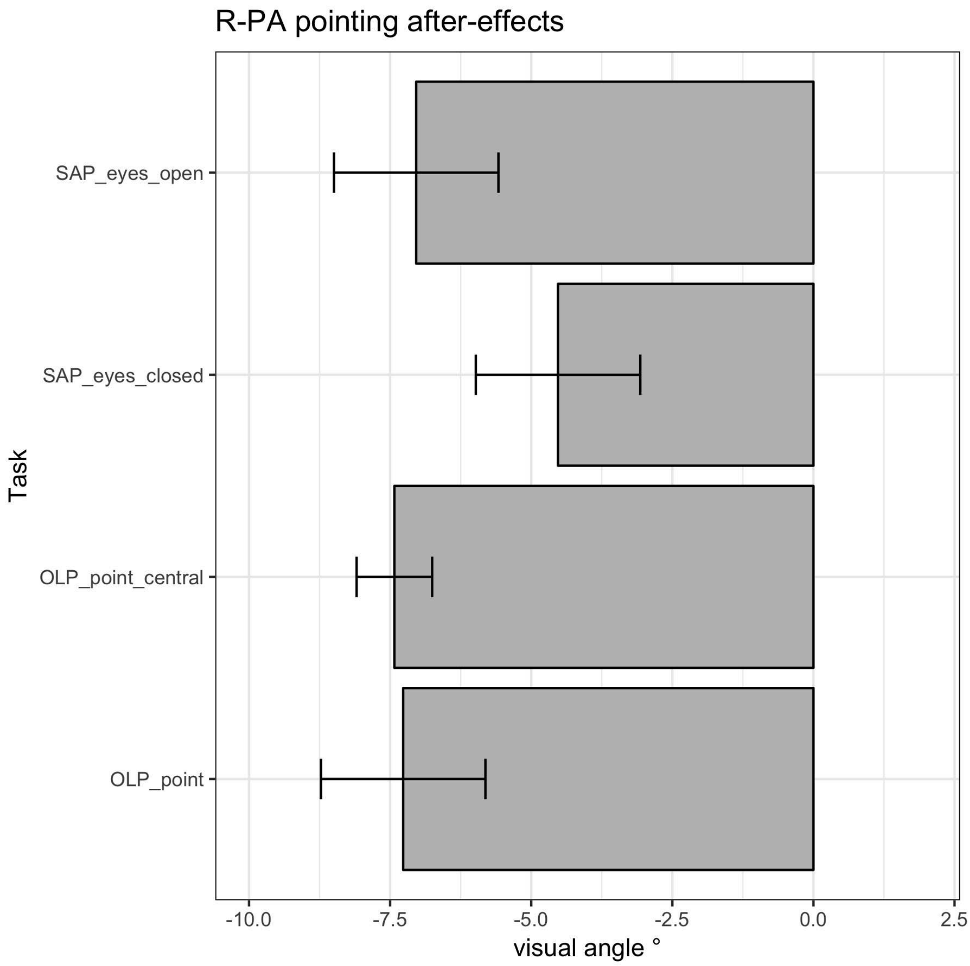

Figure 10: Mean pointing after-effects in degrees of visual angle following R-PA (hand unseen in all tasks). Error bars are 95% confidence intervals. Negative values = leftward after-effect. (OLP point central = OLP targets that lie within the 95% confidence interval of baseline observed straight ahead scores. This is included to demonstrate a lack of position effect of OLP targets and the validity of its comparison with SAP.).

Finger localisation (exposed & unexposed hand).

An omnibus ANOVA including the factors task Element (eye location during blank screen, eye location during un-numbered onscreen stimulus, eye location during numbered onscreen stimulus, verbal location), Time (post-sham, post-exposure) and Shift (R-PA, R-EMP) revealed no interaction involving Element on the finger localisation responses. Thus, we collapsed the means of the different measures.

A repeated-measure ANOVA with the factors Time, Shift, and Hand (exposed, unexposed) revealed a significant three-way interaction, ($F(1,17) = 10.7$, $p = .004$, $\eta_G^2 = .012$), see figure 11. Bonferroni-corrected Tukey contrasts revealed a predicted significant after-effect of R-PA (M = 4.59, 95% CI [2.71, 6.48], p < .001) on the exposed hand, but against prediction, no significant after-effect of R-PA for the unexposed hand (M = 1.76, 95% CI [-0.134, 3.65], *p* = .183). Also against predictions there were no significant after-effects of R-EMP for either the exposed (M = 0.593, 95% CI [-1.29, 2.48], *p* = .99) or unexposed hand (M = 0.937, 95% CI [-0.953, 2.83], *p* = .99). There was a difference between the exposed and unexposed hands at baseline (R-PA: M = -4.69, 95% CI [-8.84, -0.538], *p* = .034; R-EMP: M = -4.82, 95% CI [-8.97, -0.668], *p* = .025). However, there was no difference between baseline localisation errors for the exposed hand across exposure conditions (M = 1.06, 95% CI [-1.24, 3.37], *p* = .99) nor between the baseline localisation errors for the unexposed hand across exposure conditions (M = 1.19, 95% CI [-1.11, 3.50], *p* = .99). Post exposure there continued to be no difference across exposure conditions for the unexposed hand (M = 2.01, 95% CI [-0.289, 4.31], *p* = .282) while there was a post exposure difference between finger localisation errors for the two exposure conditions for the exposed hand (M = 5.07, 95%CI [2.76, 7.37], *p* < .001) due to the expected shift in exposed limb proprioception. There was a difference between the exposed and unexposed hand post exposure for the prism adaptation condition (M = -7.53, 95% CI [-11.7, -3.38], *p* < .001). For the EMP condition there was no significant difference between the exposed and unexposed hand after prism adaptation (R-EMP M = -4.48, 95% CI [-8.63, -0.324], *p* = .053). In sum, the only hand-condition combination that created an after-effect was R-PA and the exposed hand.

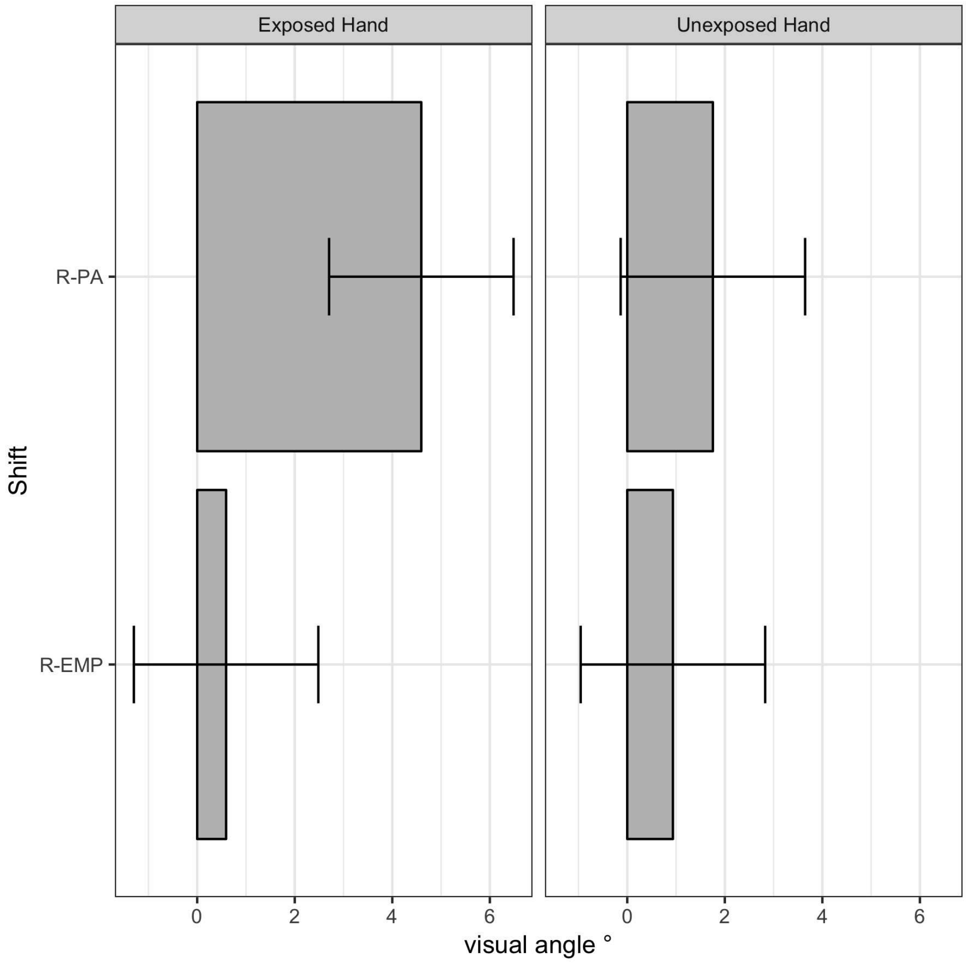

Figure 11: Finger location group mean after-effect in degrees of visual angle. Error bars are 95% confidence intervals. Positive values = rightward after-effect.

4. Discussion

The current research aimed to better understand the effects of prism adaptation on visual localisation and oculomotor proprioception, to determine if these changes are due to adaptation per se or whether there is a contribution from eye muscle potentiation, and to examine how visual perceptual and oculomotor changes interact with and contribute to arm proprioceptive and total after-effects. We found significant SAP (eyes open and closed) and OLP after-effects following R-PA but not R-EMP. The leftward after-effect for SAP with the eyes closed was significantly smaller following R-PA than those for OLP and SAP with the eyes open. We found significant rightward eye position in orbit after-effects in only one task (SAP as measured with eyes open) following R-EMP, but not in any task following R-PA. Neither exposure condition resulted in a shift in visual perception of straight ahead.

As expected, visual localisation of the finger of a passively moved arm shifted rightward for the exposed arm following R-PA. There was no shift in visual localisation for the unexposed arm following R-PA, nor for the exposed or unexposed arms following R-EMP.

VSA after-effects have been reported in some previous studies, but not others. We used more than one test of visual after-effect within the same session and found no changes in either eye position in orbit or visual perception following R-PA. If visual and proprioceptive after-effects conformed to the concept of linear additivity our observation of larger OLP than SAP with the eyes closed would have been accompanied by evidence for some change in the localisation of visual targets or direction of gaze. The failure to observe such effects may reflect the dynamic nature of sensorimotor interactions and the difficulty capturing its multiple underlying mechanisms with static behavioural measures. The timing of the test, and the type and number of tests employed, may be important for probing the visual shift after-effect. These have not been rigorously examined to date. We do not dispute the assertion that successful adaptation restores sensory harmony – presumably what the linear additivity equation aims to represent. However, our results refute the conventional account of direct linear additivity between visual and proprioceptive after-effects.

Against predictions, no shifts in eye position or perceptual judgements were observed as a result of R-EMP exposure when measured during the VSA task. However, during the SAP with eyes open task, eye position following R-EMP was deviated to the right when attempting to look straight-ahead of body midline both prior to and simultaneous with pointing. Pointing accuracy during the same task was not impaired by R-EMP. (Note, the overall lack of a pointing after-effect following R-EMP precludes the possibility that arm muscle potentiation took place, and is as we expected because arm movements during pointing involved movement in multiple planes (horizontal, vertical, and radial). We cannot discount the possibility that the observation of eye position change during only the SAP with eyes open task, and not the VSA task, could be to do with the amount of total prism exposure. The VSA tasks were performed after 96 exposure trials, whereas the SAP task with eyes open followed a top-up set of an additional 30 trials. Previous studies have shown that time is a determining factor in the emergence, magnitude and decay rate of eye muscle potentiation (Paap & Ebenholtz, 1976; Ronga et al., 2017). Nonetheless, the finding of a shift in eye position in SAP as measured with eyes open following R-EMP, but not following R-PA, are consistent with the results of Newport et al. (2009), and their conclusion that the ocular rotation that accompanies eye muscle potentiation does not contribute to the shift in subjective judgements of visual straight-ahead following PA.

The presence of an eye position change only in the R-EMP condition suggests that EMP either does not occur during PA or is suppressed by the PA process. Eye muscle potentiation effects are also subject to rapid decline (within 92 s following 4 min deviation) (Paap & Ebenholtz, 1976). This decay effect may account for the lack of a significant R-EMP after-effect in the finger localisation tasks as it took a few minutes to set-up the necessary equipment.

In contrast to the absence of pointing errors following R-EMP, the R-PA results revealed a pointing shift in the predicted leftward direction. This shift was largest, and similar in magnitude, when pointing straight-ahead in the dark with the eyes open and pointing toward a visual target during OLP. Pointing straight ahead with eyes closed produced smaller shifts. Despite multiple design precautions to eliminate visual environmental cues (soft blinkers around eye-tracker, dark windowless room, computer screens set to dim, matt black frame asymmetrically placed around computer screen, eyes closed unless needed for a task, jittering of annuli locations), it is nonetheless possible that cues to spatial locations in the visual scene were available to the participants. For example, a low contrast border between the touchscreen and the offset frame may have been visible. If participants used this cue when making VSA judgements, this could explain the lack of a VSA shift. Indeed, such environmental cues could have driven the difference between SAP as measured with eyes open and eyes closed. However, there are many previous studies that report zero perceptual VSA shift in the absence of environmental cues (e.g., in the dark; Bornschlegl, Fahle, & Redding, 2012; Choe & Welch, 1974; Morton & Bastian, 2004). Furthermore, when we examined the raw positioning errors for the VSA judgements, these did not appear to correspond to the direction and magnitude of the offset border, which would be the case if participants were using the border as a spatial cue. Thus, while the visual context may have biased results it is unlikely to be solely accountable for the pattern of results found here. Since thirty top-up trials of prism adaptation intervened between the SAP with eyes closed measure, and the SAP with eyes open and OLP measures, it is possible that the larger pointing after-effect for the latter two measures were simply due to further adaptation. However, on the assumption that additional exposure is not the sole explanation for the larger pointing after-effects and that the relative errors of the three pointing conditions are informative regarding underlying PA mechanisms, there is an alternative explanation that may prove insightful.

A key difference between the two SAP tasks that might be relevant for explaining the differences between their recorded after-effects is the presence (SAP eyes closed) and absence (SAP eyes open) of the stereotypical ocular movement that accompanies closing the eyelid (Collewijn, Van der Steen, & Steinman, 1985; Takagi, Abe, Hasegawa, & Usui, 1992). That eyelid opening/closing involves a stereotypical movement suggests it is a useable signal. In support of this account, a difference in behaviour when the eyes are open versus closed has been demonstrated in the complete absence of visual information under conditions that controlled for oculomotor commands and retinal stimulation (Yelnik et al., 2015). Specifically, they studied walking performance in healthy people who walked with their eyes open, their eyes closed, their eyes open while wearing blacked-out goggles, and their eyes open while wearing whitened-out goggles. They found that walking with the eyes closed impaired walking performance, however performance deteriorated further with the eyes open in both goggle conditions. These findings demonstrate that simply leaving the eyes open signals to the CNS to include (ocular) proprioceptive system inputs in any necessary computation of total state estimates. Further, there is evidence that perturbing ocular afferents up-weighs the estimated reliability of the ocular proprioceptive signal following adaptation (van Donkelaar, Gauthier, Blouin, & Vercher, 1997) and brain injury (Balslev, Himmelbach, et al., 2012). These pieces of evidence tell us that regardless of the visual information available the status of the eye (open versus closed) influences body movement, that this influence stems from the proprioceptive system and that ocular proprioception may be relied on more heavily to control eye movements and eye position during situations of signal conflict. Thus, it is possible that the difference between the after-effects of SAP as measured with eyes open and eyes closed may stem from ocular proprioception.

For the finger localisation task, we predicted that there would not be a shift in passive arm proprioception for the unexposed arm following R-PA. We therefore reasoned that, if a shift in eye position in orbit were observed in the finger location task for the unexposed hand, it would be due to changes within the oculomotor system (just as changes in the shift of subjective body midline are proposed to underlie changes in conventional VSA tests). We further reasoned that any such changes would need to differ from any EMP shifts observed in the same task in order to attribute them as an adaptation specific after-effect. We found no shift in visual localisation of the unexposed hand following R-PA, nor for either hand following R-EMP. However, as a leftward shift was observed in finger localisation for the exposed hand following R-PA, it suggests that leftward shift was entirely due to a change in arm proprioception. Alongside the absence of significant VSA shifts, and the relative differences in the pointing after-effects (i.e., the pointing tasks with active movements and the availability of vision - OLP and SAP as measured with eyes open - being of similar magnitude and larger than SAP as measured with eyes closed), the lack of an eye position change in the passive finger localisation of the unexposed hand suggests that active arm motor commands are necessary for a detectable change in the oculomotor system to take place. That is, the availability of vision and an active arm motor command are both prerequisites for updated oculomotor behaviour to manifest.

If the interpretation that (part of) the difference between the two SAP tasks is driven by an ocular proprioceptive change and that an active arm motor command is required for this change to manifest is correct - why might there be change in ocular state estimates but no detectable change in eye position or visual localisation of straight-ahead? The lack of detectable eye position change may be the result of the relationship between the two extra-retinal sources of eye position - ocular proprioception and corollary discharge. While corollary discharge is understood to be the dominant source of eye position information during on-going movements, there is a growing body of work showing that ocular proprioception contributes to the calibration of a state estimate of gaze direction when it conflicts with the state estimate derived from corollary discharge signals (Balslev, Newman, & Knox, 2012; Gauthier, Vercher, & Zee, 1994; Lewis et al., 2001). It has also been demonstrated that in the absence of visual information ocular proprioception can dominate over the corollary discharge signal after as few as 5 saccades (Poletti et al., 2013). From this we might infer that the two sources of eye position information influence each other and that the weighting of each source will vary depending on the circumstance. Under normal circumstances, there should be little moment-to-moment conflict between ocular proprioception and corollary discharge but PA is a dramatic circumstance. Therefore, the relative influence of a PA induced ocular state estimate change on pointing, and the emergence or not a VSA shift, may relate to the reliability weightings of each source of eye position according to the task at hand (as well as contextual factors such as the time since adaptation). There are also gaps in our understanding of the physiological underpinning of the relationship between these two sources of eye position information. For example, the two putative receptors (palisade endings and muscle spindles) on the eye muscles are associated with different types of eye muscle fibres (respectively, fatigue resistant non-twitch fibres that do not generate action potentials and fast twitch fibres that do) that in turn are associated with different eye movement types (fixation and smooth pursuit; and saccades respectively) (Bruenech & Kjellevold Haugen, 2015; Büttner-Ennever, 2007; Spencer & Porter, 2005). Further knowledge of the relationship between these sources of eye position, and the relevant physiology, may help in understanding the visual response to PA.

5. Limitations

Some of our design choices may have influenced the pattern of results and should be addressed in future studies. First, we chose for all participants to undergo EMP followed by PA exposure, rather than counterbalance the order of these conditions. This is because there is evidence that PA can have lasting effects on pointing behaviour and sensorimotor interaction (Hatada et al., 2006). Indeed, even if PA is immediately followed by de-adaptation (pointing while wearing neutral lenses), participants will show faster adaptation to a subsequent session (Morehead, Qasim, Crossley, & Ivry, 2015). Rather than risk PA from contaminating subsequent EMP exposure, we decided that all participants would undergo PA in the second week. A future study could instead counterbalance the order of sessions, or use a between-subjects design, to control for potential order effects. A second limitation is that all participants completed the after-effect tasks in the same set order (i.e. these were not counterbalanced). We did this because it was not possible to cover all possible combinations of orders with the number of participants we tested. However, this might have led to artificially small SAP, OLP and localisation of the unexposed hand after-effects (because these tasks were preceded by other after-effect tasks, meaning that the after-effect had time to ‘wash out’). Our data suggest that any such wash-out was negligible, because (for example) the pointing magnitudes of SAP as measured with eyes open and OLP were the same, even though the OLP task was performed later. Future studies would be enhanced by increasing sample size and counter-balancing after-effect tasks between participants.

6. Conclusion

We attempted to shed light on the mechanisms underpinning changes in visual straight-ahead following PA and how they influence and interact with arm proprioceptive and the total shift. Like many previous studies, we found no significant change in visual straight ahead following prism adaptation. Adding to this evidence, we demonstrated this for both oculomotor and perceptual measures of straight ahead in the same study, which means it is unlikely that the absence of a significant effect is due to inappropriate choice of measure. Our results also add to existing evidence that challenges the concept that total after-effects are a simple combination of visual and arm-proprioceptive after-effects. Furthermore, our results provide evidence that EMP cannot explain PA after-effects, but may in fact be suppressed by PA.

Although we found no effects of PA on our measures of visual straight ahead, we found that measuring SAP with the eyes open resulted in larger after-effects than measuring SAP with the eyes closed, and comparable after-effects to OLP. This suggests that the oculomotor system *is* altered by prism adaptation but that this alteration is only apparent in interaction with an arm motor command (itself acting on altered arm proprioception) when vision is available.

Codes and data for this paper can be found at Open Science Framework:
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