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Citation for published version:

McIntosh, R, Brown, B & Young, L 2019, 'Meta-analysis of the visuospatial aftereffects of prism adaptation, with two novel experiments', *Cortex*, vol. 111, pp. 256-273. <https://doi.org/10.1016/j.cortex.2018.11.013>

Digital Object Identifier (DOI):

[10.1016/j.cortex.2018.11.013](https://doi.org/10.1016/j.cortex.2018.11.013)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Cortex

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Meta-analysis of the visuospatial aftereffects of prism adaptation, with two novel experiments

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Acknowledgements

We are grateful to Yves Rossetti for the loan of the prism glasses for Experiment 2, and to all the researchers who provided raw data for the meta-analysis.

Open-data: Full raw data with analysis code are available at: <https://osf.io/u65by/>.

Abstract

We present a meta-analysis of the effects of visuomotor adaptation to leftward displacing prisms on visuospatial judgements in healthy people, as assessed by perceptual (landmark) and manual versions of the line bisection task. To supplement previously published datasets, we report two novel experiments: Experiment 1 ($n=12$) found null effects of adaptation to 10° leftward prisms on spatial bias in the landmark task, and Experiment 2 ($n=24$) found null effects of 12° leftward prisms on spatial bias in a computerised line bisection task. Including these data, we considered 17 experiments for the landmark task (total $n = 256$), and 12 experiments for line bisection (total $n = 172$), in which participants were adapted for between 7 and 20 minutes to prism strengths from 8 to 17° . A random-effects meta-analysis, with prism strength and exposure duration as moderators, confirmed robust rightward shifts in visuospatial judgements following leftward prism adaptation. The average standardised effect sizes (Cohen's d) were similar between tasks, increasing by around 0.1 per degree of prismatic displacement, and being boosted by a long (10 minute +) period of prism exposure. However, the quality of evidence and precision of prediction was superior for the landmark task, with a higher signal-to-noise ratio within studies, and less heterogeneity between studies. We suggest that line bisection responses may be contaminated by sensorimotor aftereffects, and that the landmark task is a more suitable method for measuring true visuospatial aftereffects of prism adaptation. To harness these effects, we recommend that researchers should expose participants to 15° (or higher) leftward prisms for more than ten minutes, with upwards of 250 pointing movements. Power calculations should take account of heterogeneity in the true effect size between studies; and further investigation of the factors underlying this heterogeneity will help to refine optimally-effective methods.

Keywords: prism adaptation; landmark task; line bisection; meta-analysis; neglect; pseudoneglect.

1. General introduction

The original report of amelioration of left neglect following adaptation to (10°) rightward-displacing wedge prisms (Rossetti et al., 1998), was followed by the finding that prism adaptation could induce previously-unsuspected visuospatial changes in healthy adults too (Berberovic & Mattingley, 2003; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel, Pisella, et al., 2003). These were a miniature mirror of the neglect effects: just as rightward adaptation could temporarily reduce the pathological rightward bias of neglect, leftward adaptation could reduce or reverse the more subtle leftward bias ('pseudoneglect') that typifies healthy performance on manual line bisection, and its perceptual counterpart the landmark task (Jewell & McCourt, 2000; Milner, Harvey, Roberts, & Forster, 1993). Colent and colleagues (2000), found that adaptation to (15°) leftward prisms shifted the perceived midpoint (point of subjective equality in a landmark task) of a 250 mm line rightward by an average of 1.12 mm (SD 0.82) in a group of seven adults. The shift was less than one percent of the line half-length, but it was statistically very strong (Cohen's $d = 1.37$). This study found no comparable effects of prisms on manual line bisection, but a second study did show significant rightward shifts of bisection error after leftward prism adaptation, in addition to changes on the landmark task (Michel, Pisella, et al., 2003). These findings potentially establish a non-lesion model of neglect, and provide a powerful manipulation for studying spatial representation, and its relation to low-level sensorimotor mappings, in the healthy brain.

At least eleven published studies, often with more than one experiment, have now followed the same general template (Berberovic & Mattingley, 2003; Colent et al., 2000; Guinet & Michel, 2013; Herlihey, Black, & Ferber, 2012; Michel, Pisella, et al., 2003; Michel & Cruz, 2015; Nijboer, Vree, Dijkerman, & Van Der Stigchel, 2010; Schintu et al., 2014, 2017; Striener & Danckert, 2010; Striener, Russell, & Nath, 2016). Prism adaptation is induced by repetitive pointing to dots, with visual feedback of the hand during the second half of the reach (so-called 'concurrent' exposure; Redding, Rossetti, & Wallace, 2005).¹ Effective adaptation is confirmed by checking for the expected sensorimotor aftereffect, through pointing responses made without visual feedback, or visual or proprioceptive straight-ahead judgements. Leftward displacing wide-field wedge prisms are invariably used,

¹One study (Herlihey et al., 2012) contrasted concurrent exposure with 'terminal' exposure in which only the final finger position is visible.

though the strength of prisms may vary. Published studies include optical shifts in the range of $8-17^\circ$, equivalent to $\sim 15-30^\Delta$ (prism dioptres, where 1 prism dioptre would induce a 1 cm shift of an object viewed at 1 m). Four studies have included rightward prism adaptation for comparison (Berberovic & Mattingley, 2003; Colent et al., 2000; Schintu et al., 2014, 2017). One study has incorporated a sham-adaptation (no prism) condition, to control for procedural factors other than prism strength or direction (Guinet & Michel, 2013).

All of these studies used one or both of the landmark and line bisection tasks to test for visuospatial aftereffects of prism adaptation. The measure of performance for line bisection was always the mean directional bisection error (DBE) from the true midpoint; but two different measures of landmark performance have been used. Most studies make use of all the landmark data, fitting a sigmoid function to the probability that a participant judges the left of the line to be shorter, according to the position of the transection mark. This allows for the estimation of a point of subjective equality (PSE) at which the participant is equally likely to respond in either direction, a spatial measure of bias, expressed in units of distance, that is a perceptual counterpart of the manual DBE. Other studies collate responses from ‘critical’ trials only, usually those lines transected at the true midpoint, giving a proportional bias (Herlihey et al., 2012; Nijboer et al., 2010; Striemer & Danckert, 2010; Striemer et al., 2016).

This literature has been reviewed recently, and the central finding that leftward prism adaptation can induce rightward spatial shifts seems to be well-established (Michel, 2016). In this paper, rather than repeating prior narrative summaries, we aim for a quantitative meta-analysis of the effects of prism adaptation on normal visuospatial judgements, as assessed by landmark or line bisection tasks. In any meta-analysis, we should consider the possibility of a ‘file-drawer effect’, whereby the literature could be biased towards positive findings, if null results are less likely to be published. We have two relevant experiments in our own file-drawer, with methods comparable to those of the above studies.² These experiments, which date from 2006-2007, obtained null effects of leftward prism adaptation on landmark and line bisection tasks respectively. Neither finding is sufficient to overturn the weight of evidence for positive effects, which is the main reason that they have not been published previously. However, we can factor them into our meta-analysis, for a more balanced overview of the total evidence. We return to our meta-analysis after reporting these two experiments.

² We would be keen to hear from other researchers with unpublished data on this topic.

2. Experiment 1: Introduction

Like the hemispheric organisation of spatial representation itself, the effects of prism adaptation in the normal brain may be asymmetric: leftward prisms induce a rightward shift in spatial judgements, but rightward prisms seem not to have the converse effect. This was a key feature of Colent and colleagues' original report, and has been replicated by Schintu et al. (2014; see also Schintu et al., 2017), and in the peripersonal space condition of Berberovic & Mattingley (2003). However, the asymmetry has been inferred from significant effects of leftward prisms and null effects of rightward prisms, yet without testing the critical difference between prism directions; this is also true for studies extending the pattern to number bisection, and the grayscales task (Loftus et al., 2009; Loftus, Nicholls, Mattingley, & Bradshaw, 2008). Moreover, Berberovic & Mattingley (2003) found that rightward prisms did induce a significant shift for the landmark task when presented in extrapersonal space. This shift was to the right; that is, in the same direction as the shift induced by leftward prisms. Berberovic & Mattingley (2003) suggested some creative, albeit tentative, interpretations for this unexpected finding.

However, there is a procedural confound that could potentially account for visuospatial aftereffects that would not differ between leftward or rightward prisms, as they would not result from sensorimotor realignment at all. In a study unconcerned with prisms, Manly, Dobler, Dodds, & George (2005) tested ten shift-workers after periods of sleep, or sleep-deprivation, and found evidence for reduced pseudoneglect (i.e. more rightward bias) in the sleep-deprived condition. They also noted a rightward drift across the forty-minute session, in both conditions, and they replicated this latter, 'time-on-task' effect across a longer, sixty-minute session, in ten healthy adults (see also Benwell, Thut, Learmonth, & Harvey, 2013; Dufour, Touzalin, & Candas, 2007). These findings could be understood in terms of a right-hemisphere association with sustained attention and alertness (e.g. Cohen et al., 1988; Lewin et al., 1996; Robertson, 1993). In the alert state, the leftward orienting tendency of the right hemisphere would predominate, giving rise to pseudoneglect; but, as alertness declined with sleep deprivation and/or over a long testing session, this dominance would wane, and be overtaken by the rightward bias of the left hemisphere. In prism adaptation studies, although the participants do not perform a single task continuously, they typically perform similar pre-tests and post-tests, separated by a repetitive adaptation

procedure lasting up to 20 minutes. If Manly and colleagues are correct, then some degree of rightward shift might be expected in prism adaptation studies, merely due to declining alertness over the course of a repetitive testing session.

The purpose of Experiment 1 was to re-assess the consequences of adaptation to leftward prisms for visuospatial judgements in the landmark task, and to evaluate the contribution of a lengthy, repetitive testing session. We adapted young healthy adults to leftward prisms in the middle third of a sixty-minute session, with a landmark task performed pre- and post-adaptation. The same participants also completed an identical testing session, but with a sham procedure (plain lenses) in place of prism-adaptation. This within-subject control condition should allow us to isolate the effects on spatial perception that are specific to the prism adaptation treatment from any more general influences of the testing session.

3. Experiment 1: Methods

Participants

Twelve young adults (8 female, 4 male), aged 20-33 (median 21) took part; all were right-handed by self-report. All participants provided informed verbal consent, and the protocol was approved by the Psychology Research Ethics Committee, University of Edinburgh.

Design and set-up

Experiment 1 was fully within-subjects. Each participant took part in two similar, hour-long testing sessions. The two sessions were run at the same time of day, and separated by at least one week. Each session was divided into seven blocks, as follows: pre-adaptation landmark blocks 1 and 2 (15 minutes); pre-adaptation open-loop pointing (2 minutes); adaptation (closed-loop pointing) (20 minutes); post-adaptation open-loop pointing (2 minutes); post-adaptation landmark blocks 1 and 2 (15 minutes). The only difference between the sessions was that the glasses worn during adaptation contained either 10° leftward-displacing wide-field wedge prisms (Prism adaptation condition) or plain lenses (Sham adaptation condition). The order of conditions (Prism or Sham first) was counterbalanced across participants.

Throughout all tasks, the participant sat at a table, with the head in a chin-rest, centrally facing a touchscreen (active display 34*27 cm) at a viewing distance of 50 cm. A 15

cm-deep shelf, attached to the chin-rest, blocked the participant's view of the first third of the reach-path to the screen. Below the shelf, on the table, was a computer keyboard, with which the right hand could interact. The left hand was on the participant's lap. The room was ambiently-lit, and the participant was unable to see either hand, except during the adaptation procedure, to avoid de-adaptation.

Landmark task

At the start of each block of the landmark task, the experimenter placed the participant's index and middle fingers on the left and right arrow keys of the keyboard, to which slightly raised stickers were attached. The participant was shown a series of horizontal white lines against a black background. Each line was 300 mm long and 1 mm thick, presented in the vertical centre of the screen, and transected by a 13 mm vertical line, 1 mm thick. For each transected line, the participant was required to press the corresponding arrow key to indicate which side was shorter (or, in different blocks, longer). The line disappeared when a response was recorded, followed by the next line after 500 ms. Lines were selected randomly without replacement from a list of 400 stimuli, and the task was performed continuously for 7.5 minutes, or until all 400 lines had been shown. Lines were transected at either 1, 2, 4 or 8 mm to the left or right of centre, with 40 lines for each of these conditions, and 80 lines transected at true centre. The horizontal position of the line was jittered slightly from trial to trial: 20% of lines of each type were shifted 1.5 mm left, 20% 3 mm left, 20% 1.5 mm right, 20% 3 mm right, and 20% were centred on the screen. Participants worked at their own pace, so the total number of landmark judgements made across the pre- or post-adaptation pairs of blocks varied, but it was never less than 187 (mean 550, SD 156).

Open-loop pointing

Immediately prior to and following the adaptation block, the participant pointed, without visual feedback, to a red dot (10 mm diameter) shown centrally on the screen. The participant pressed the space button to show each dot, and prepared to point towards it. The experimenter then blocked the participant's view with a cardboard occluder, and gave the cue to respond. The dot disappeared when the participant touched the screen, but the experimenter did not

withdraw the occluder until the hand was returned to the keyboard. The sequence was performed six times.

Adaptation (closed-loop pointing)

The middle block in each session was the adaptation procedure, in which the participant made fast pointing movements to the screen to touch a red dot (10 mm diameter), shown randomly 10° to the left or right of the midline. The hand became visible during the last two-thirds of the reach (concurrent exposure). The dot disappeared when the screen was touched, and the participant returned their hand to the space-bar to show the next dot. They did this continuously for 20 minutes, whilst wearing a pair of glasses containing either 10° leftward prisms or plain lenses. Participants worked at their own pace, so the total number of pointing movements made in the adaptation period varied, but it was never less than 331 (mean 635, SD 166).

Data analysis

For open-loop pointing blocks, the mean horizontal deviation of the pointing response from the dot centre was calculated, with leftward errors negative and rightward errors positive. The pre-adaptation block mean was subtracted from the post-adaptation block mean to give the adaptation after-effect, which was then expressed in degrees of visual angle.

The landmark task was analysed in two ways. For comparability with some prior studies, we analysed the percentage of critical trials (with the transection at the true centre) for which the participant indicated that the left side was shorter. Higher values indicate a greater tendency to underestimate the left side relative to the right. Our second, preferred, analysis was based on all of the landmark data, fitting a binomial logistic regression to model the probability of a left-is-shorter response according to the transection location. Provided that the fit was significant ($p < .05$ by Wald test) – which it was in every case – then the model was used to calculate the point of subjective equality (PSE; the transection point at which the probability of a left-is-shorter response is .5) and the just noticeable difference (JND; half of the transection distance between .75 and .25 probability of a left-is-longer response). PSE and JND represent the bias and the sensitivity of perceptual judgements respectively.

For the graphical presentation of results, boxplots are used as the standard format, as not all variables were normally-distributed. Where normality is not violated, we may additionally report means and SDs and use these to calculate standard effect sizes (Cohen's *d*).

4. Experiment 1: Results

Open-loop pointing (Figure 1a)

The average sensorimotor after-effect was slightly negative in the Sham condition, indicating an unexpected but small leftward shift of pointing responses following sham adaptation. The shift was positive in the Prism condition, consistent with a rightward after-effect of leftward prism adaptation. Relative to the Sham control, the aftereffect was robustly rightward, reflecting ~42% of the 10° prismatic shift (mean 4.19°, SD 1.79, *d* = 2.34).

Landmark task

There was no significant directional bias at pre-test on the landmark task, in either in the Prism or Sham adaptation conditions, whether judged by 'left-is-shorter' responses on critical trials (Prism condition pre-test mean 49.03%, CIs 43.71 to 54.35; Sham condition pre-test mean 49.24%, CIs 43.67 to 54.80), or by PSE (Prism condition pre-test mean 0.26 mm, CIs -0.19 to 0.71; Sham condition pre-test mean 0.24 mm, CIs -0.35 to 0.82). Moreover, there were no consistent changes in landmark performance after either Prism or Sham adaptation (Figure 1b-1d). The *specific* visuospatial after-effect of prism adaptation, represented by the subtraction of the aftereffect for the Sham condition from that for the Prism condition, was close to zero for both measures. The mean difference for PSE, our preferred measure of bias, would estimate the specific shift associated with prism treatment to be 0.05% of the line half-length (0.07 mm, SD 1.35, *d* = 0.05).

There was, however, an overall tendency for an increased JND at post-test in Prism and Sham conditions alike, reflecting a more shallow logistic function. This shift did not differ significantly between Prism and Sham conditions (Wilcoxon one-sample *t*-test to compare the Prism-Sham difference against zero: *n* = 12, *V* = 51, two-tailed *p* = .28). The increase in JND between pre- and post-tests, collapsed across adaptation conditions, was

significantly greater than zero (Wilcoxon one-sample t-test, $n = 12$, $V = 75$, two-tailed $p = .002$). This reduced perceptual sensitivity probably reflects reduced alertness and motivation in the second half of each testing session relative to the first.

5. Experiment 1: Discussion

Experiment 1 did not find any evidence of rightward visuospatial aftereffects of leftward prism adaptation, despite effective sensorimotor adaptation. There was a significantly reduced sensitivity (increased JND) of landmark judgements at post-test, which was independent of the prism treatment, as it was equally present in the Sham condition. Previous studies have not analysed the sensitivity of landmark judgements, but our result would be consistent with reduced alertness and motivation due to time on task. Nonetheless, this general reduction in sensitivity was not associated with any rightward shift (cf. Benwell et al., 2013; Dufour et al., 2007; Manly et al., 2005).

6. Experiment 2: Introduction

Given the null outcome of Experiment 1, we designed a follow-up study to re-examine the aftereffects of leftward prism adaptation on visuospatial judgements in the healthy brain. Our design included several features to enhance the likelihood of detecting an effect, as well as some procedural controls to eliminate potential confounds that could lead to spurious positive findings. First, we adapted twice as many participants ($n = 24$) to a leftward prismatic shift as used in Experiment 1. Second, we used a stronger prismatic shift, of 12° . Third, for half of the participants in the Prism condition, we used a Multi-step adaptation procedure, whereby participants were adapted to the 12° shift via graded exposure to smaller incremental shifts. This has been reported to enhance the sensorimotor aftereffect as compared with the standard Single-step exposure to the same prism strength (Michel, Pisella, Prablanc, & Rode, 2007). As in Experiment 1, we included a Sham adaptation condition to control for other factors, such as declining alertness during the testing session; in Experiment 2, this control condition was performed by a separate group of 12 participants. However, where the protocol of Experiment 1 had been deliberately protracted, to encourage declining alertness, we did not make Experiment 2 any longer than necessary.

Experiment 2 studied the line bisection task, rather than landmark judgements, because we considered that the direct setting of the midpoint might provide a more efficient estimation of spatial bias. Here, however, we must be cautious, because line bisection usually involves a manual response. After adaptation to leftward prisms, people generally reach further rightward than they intend to, so bisection responses might inherit some rightward shift as a direct expression of the sensorimotor aftereffect. Perceptual monitoring will tend to correct for this unwanted bias, and some studies have emphasised slow and small amplitude bisection responses to try to ensure that it does (e.g. Colent et al., 2000; Michel, Pisella, et al., 2003). But there may nonetheless be some contamination from sensorimotor aftereffects. We therefore adapted the line bisection task, to try to avoid contamination. Bisection responses were made by moving a cursor to the perceived midpoint of the line, using a computer mouse held out of view in the right hand. The control over the cursor is in screen-relative coordinates, and under visual monitoring, so it should be relatively unaffected by any change in the sensorimotor mapping of proprioceptive coordinates to visual space.

Finally, we used a set of bisection stimuli (see Methods) that allowed us to apply the endpoint-weightings analysis of bisection behaviour developed by McIntosh, Schindler, Birchall, & Milner (2005). In this analysis, the position of the response relative to the objective centre of the line (i.e. DBE) is not important. The focus is instead on how the response varies as a function of the positions of the left and right endpoints of the line, which are manipulated independently. The endpoint weightings analysis has been described in detail and validated elsewhere (McIntosh, 2006, 2017; McIntosh, Ietswaart, & Milner, 2017; McIntosh et al., 2005b). It proposes to measure attentional allocation to each end of the line (the endpoint weightings). This leads to two composite measures of performance: the endpoint weightings bias (EWB), which indexes the difference in attentional allocation to the two ends of the line; and the endpoint weightings sum (EWS), which indexes the total amount of attention. This analysis is not only more sensitive than DBE to the rightward spatial bias of neglect, it is also more sensitive to the leftward bias ('pseudoneglect') of healthy controls (McIntosh, 2017; McIntosh et al., 2005b). It should also therefore be more sensitive to any visuospatial aftereffect of leftward prism adaptation, though we will also analyse the traditional measure of DBE for comparability with prior studies.

7. Experiment 2: Methods

Participants

Three groups of twelve young adults took part (Single-step Prism, Multi-step prism, and Sham adaptation). All three groups had a median age of 21 years (Single-step, range 16-29; Multi-step, range 17- 24; Sham, range: 18-31). The Prism groups each had eight females and four males, and the Sham group had nine females and three males. All participants were right-handed, with a laterality quotient of at least +60 on the Edinburgh Handedness Inventory (Oldfield, 1971). All participants provided informed verbal consent, and the protocol was approved by the Psychology Research Ethics Committee, University of Edinburgh.

Design and set-up

Each participant completed the following tests in a single session: open-loop pointing (2 minutes); line bisection task (10 minutes); adaptation (closed-loop pointing) (10 minutes); line bisection task (10 minutes); open-loop pointing (2 minutes). The only difference in procedure between groups was in the adaptation procedure (see below).

As in Experiment 1, the participant was seated at a chin-rest, centrally facing a touchscreen (active display 34*27 cm) at a viewing distance of 50 cm, with a 15 cm-deep shelf, attached to the chin-rest, occluding the first third of the reach-path to the screen. Below the shelf, on the table, was a central start button (during pointing blocks) or a computer mouse (during line bisection), with which the right hand could interact. The left hand was on the participant's lap. The room was ambiently-lit, and the participant was unable to see either hand, except during the adaptation procedure, to avoid de-adaptation.

Open-loop pointing

In the open-loop pointing blocks, the participant pointed to a white dot (7 mm diameter) shown centrally on the screen. The participant wore a pair of LCD shutter glasses (PLATO, Translucent Technologies), which were opaque until the participant depressed the start button with the index finger. This triggered the appearance of the target dot, and the participant was required to point towards the dot with a single fast movement. The release of the start button

turned the LCD glasses opaque, so the reach was performed without visual feedback. The glasses remained opaque until the hand returned and pressed the start button for the next trial. The sequence was performed ten times.

Line bisection task

For line bisection, the screen was moved to a further viewing distance (60 cm), so that its bottom edge was in view. The participant was shown a series of (1 mm thick) white horizontal lines varying in length from 80-240 mm (see below). The vertical position of the line was jittered across trials between 20 mm below and 40 mm above screen centre. A short white vertical-line cursor (10 mm high) started at a random position along the bottom edge of the screen, and the participant was required to use the mouse, with the unseen right hand, to move the cursor to the middle of the line, clicking when they were satisfied with its position. The horizontal line then disappeared, a green box appeared at a random position along the bottom edge of the screen, and the participant had to move the cursor to the box in order to trigger the next trial.

There were nine stimulus lines, created by the factorial combination of three possible horizontal positions of the left endpoint of the line (-40, -80 and -120 mm from the screen centre) with three positions of the right endpoint (+40, +80 and +120 mm from the screen centre). Each line was shown ten times within a block of 90 trials, in a randomly shuffled order. This stimulus set followed the design recommended for an ‘endpoint weightings’ analysis, allowing the influences of the left and right endpoints on the response position to be disentangled (McIntosh, 2006, 2017; McIntosh et al., 2017; McIntosh, Schindler, Birchall, & Milner, 2005a).

Adaptation (closed-loop pointing)

The middle block in the session was the adaptation procedure, in which the participant made fast pointing movements to the screen to touch a white dot (7 mm diameter). The hand was visible during the last two-thirds of the reach (concurrent exposure). The dot disappeared when the screen was touched, and the participant returned their hand to the start button to show the next dot. They did this for six consecutive blocks of 20 trials. Within each block,

the target appeared ten times at 10° to the left of the midline, and ten times at 10° to the right, in a randomly-shuffled order.

In the prism conditions, participants were adapted to leftward-displacing wide-field prisms. Single-step participants wore a pair of 12° prism glasses in all six blocks. Multi-step participants wore a pair of 2° prism glasses in the first block, which were switched in successive blocks for prisms of a 2° greater leftward shift, so that the participant was wearing 12° prisms in the final block, via six incremental steps of 2° . All of the prism glasses were weighted equally. The Sham adaptation group wore glasses with plain lenses in every block. In between blocks, participants were asked to close their eyes, whilst the glasses were changed over, even though the same glasses were replaced each time in the Single-step and Sham conditions.

Debrief

We questioned participants at the end of the session as to whether they noticed how the glasses had affected their vision. We then informed them that the glasses had shifted their vision to one side and asked them to guess the direction of the shift: 9 out of 12 participants in the Single-step group guessed leftward, while only 6 and 5 out of 12 participants in the Multi-step and Sham groups did so. This generally supports the idea that the Multi-step group had less awareness of the prismatic shift, as suggested by Michel et al. (2007).

Data analysis

Open-loop pointing was analysed in the same way as for Experiment 1, with leftward errors signed negative and rightward errors positive, and expressed in degrees of visual angle.

The line bisection task was analysed in two ways. First, the average horizontal position of the bisection response, in mm from the midline of the screen, was calculated across all 90 lines. Because the lines were on average presented symmetrically around the midline, this average coordinate is equal to the mean directional bisection error (DBE). Second, we conducted an endpoint weightings analysis (McIntosh, 2006, 2017, McIntosh et al., 2017, 2005a). For this, we regressed the response position (P) on the positions of the left and the right endpoints across all 90 lines. The regression coefficient for left and right

endpoint positions give the endpoint weightings (i.e the mean change in response that accompanies a change in that endpoint, expressed as a proportion of the endpoint change). From these endpoint weightings, we calculated two composite measures. Endpoint weightings bias (EWB: the right endpoint weighting minus the left endpoint weighting) is an index of attentional bias on the task, where rightward bias is positive and leftward bias negative. Endpoint weightings sum (EWS: the left endpoint weighting plus the right endpoint weighting) is an index of the total attention allocated to the task. Perfect performance would have an EWB of zero and an EWS of one.

8. Experiment 2: Results

Open-loop pointing

Figure 2a displays the pointing errors pre- and post-adaptation, for each adaptation condition (Single, Multi, Sham), showing the expected rightward shift following adaptation to leftward displacing prisms, absent after sham adaptation. Figure 3a shows the size of the after-effect (post-pre). The median aftereffect was 6.70° in the Single-prism, and 5.51° in the Multi-prism condition, accounting for 56% and 46% of the prismatic shift respectively. Despite the numerical trend toward a larger aftereffect in the Single-prism than in the Multi-prism condition, a Wilcoxon rank sum test did not find a significant difference ($W = 104$, $p = 0.07$). We thus simplify further statistical comparisons between Prism and Sham conditions, by combining the Single- and Multi-prism groups (i.e. $n=24$).

Line bisection

Figure 2b shows directional bisection errors pre-and post-adaptation. Across all participants ($n = 36$), the small average leftward bisection error at pre-test did not depart significantly from zero (mean -0.41 mm, 95% CIs -0.93 to 0.11 , one-sample $t(35) = -1.61$, $p = .12$, $d = -0.27$), and there was no evidence that it was altered by the adaptation procedure (Figure 3b). The mean aftereffect in the pooled Prism condition was 0.02% of the line half-length (0.12 mm, SD 0.82 , 95% CIs -0.23 to 0.46 , $d = 0.14$), and that in the Sham condition was 0.01% (0.10 mm, SD 1.02 , 95% CIs -0.55 to 0.75 , $d = 0.10$). The estimated effect size for the *specific* prism aftereffect on DBE was $d = 0.02$.

In the analysis of the same bisection data, based on the endpoint weightings method, the index of bias (EWB, Figure 2c) showed a small but statistically very robust leftward bias

(i.e. pseudoneglect) in the pre-prism block (mean -0.02, 95% CIs -0.03 to 0.02, one-sample $t(35) = -5.70$, $p < .0001$, $d = -0.95$). Again, there was no evidence of any shift in bias after adaptation, in either the Prism or Sham conditions (Figure 3c). The mean aftereffect in the pooled Prism condition (-0.003, SD 0.01, 95% CIs -0.009 to 0.004, $d = -0.17$) was closely equivalent to that in the Sham condition (-0.003, SD 0.02, 95% CIs -0.02 to 0.01, $d = -0.20$). The estimated effect size for the *specific* prism aftereffect on EWB was zero.

Finally, the index of total attention (EWS, Figure 2d) was significantly greater than one in the pre-prism block (mean 1.02, 95% CIs 1.01 to 1.03, one-sample $t(35) = 244.04$, $p < .0001$, $d = 0.67$). EWS was significantly reduced following adaptation, across all adaptation conditions (Figure 3d; mean aftereffect -0.01, 95% CIs -0.02 to -0.005, one-sample $t(35) = -3.43$, $p = 0.002$, $d = -0.57$), indicating a reduction in total attention in the post-prism block, presumably reflecting declining arousal and/or motivation in the second half of the session.

9. Experiment 2: Discussion

Experiment 2 found no evidence for rightward visuospatial aftereffects of leftward prism adaptation, despite using stronger prisms (12°), and achieving stronger sensorimotor aftereffects than in Experiment 1. The lack of directional shift was observed both for the traditional DBE measure of bisection bias, and also for the EWB measure extracted from the endpoint weightings analysis (McIntosh, 2006, 2017, McIntosh et al., 2017, 2005b). Despite using similar adaptation protocols, we did not replicate the claimed advantage for Multi-step adaptation in enhancing sensorimotor aftereffects (cf. Michel et al., 2007). If anything, our data were more consistent with older literature suggesting that larger aftereffects result from a sudden, rather than a gradual, prismatic shift (Dewar, 1971).

Because we included a Sham condition, we can also exclude any rightward shift associated with declining alertness over the course of the session (cf. Benwell et al., 2013; Dufour et al., 2007; Manly et al., 2005). However, we did observe a more general change in the quality of bisection behaviour at post-test. This was apparent as a reduced EWS, a measure that may index the total attention allocated during the bisection task (McIntosh, 2006, 2017, McIntosh et al., 2017, 2005b). The change is reminiscent of the decreased sensitivity of landmark performance seen at post-test in Experiment 1, and may likewise be attributable to a general reduction in alertness and motivation over the course of the session.

Thus, Experiment 2 did not replicate a rightward shift in bisection after leftward prism adaptation. This is despite the presence of an overall leftward bias (pseudoneglect) at pre-test, at least for the EWB measure. This is relevant to mention, because some authors have

suggested that the visuospatial aftereffects of prism adaptation depend on the baseline bias; specifically, that the visuospatial judgements of people with an initial leftward bias are shifted to the right after leftward prism adaptation, while the judgements of those with an initial rightward bias are shifted to the left (Goedert, Leblanc, Tsai, & Barrett, 2010; Herlihey et al., 2012; Schintu et al., 2017). An equivalent claim has been made with respect to the effects of time-on-task/alertness: that people biased initially leftward will shift rightward with declining alertness, and vice-versa (Benwell et al., 2013). A potential problem with these claims is that the proposed patterns could also arise from statistical regression to the mean. Assuming that the measurement of visuospatial bias is imperfect (i.e. influenced by chance factors), then if we select people with a bias in a specific direction on one run of a test, we are liable to find that they will be biased less strongly in that direction on any other run, just because of our selection policy (Campbell & Kenny, 1999). A subgroup of people selected for an initial leftward bias will be prone to shift relatively rightward at post-test, and vice-versa for an initial rightward bias, independent of any actual treatment effect.

Noting this confound, Newman et al. (2014) took methodological pains to exclude, or otherwise account for, regression artefacts, and they found no residual evidence that initial bias affects the pattern of change in performance with time-on-task. No equivalent analysis has yet been reported for prism adaptation, but none of the studies proposing distinct effects dependent on initial bias has definitively excluded regression to the mean as an alternative explanation (Goedert et al., 2010; Herlihey et al., 2012; Schintu et al., 2017). The possibility that the baseline bias of visuospatial cognition modulates the response to prism adaptation merits closer examination, but we will not consider it further here.

Overall, Experiment 2 found no *specific* effect of prism adaptation on line bisection. We are now in a position to weigh this null result, and that of Experiment 1, alongside other empirical evidence concerning the visuospatial aftereffects of leftward prisms.

10. Meta-analysis of the visuospatial aftereffects of prism adaptation

Description of datasets

To the best of our knowledge, we reviewed all of the available evidence on the effects of adaptation to leftward prisms on landmark and line bisection tasks in healthy participants. We included data from eleven published studies, and the two experiments reported in the present paper. We excluded three other studies that used very different adaptation and bisection procedures (Fortis, Goedert, & Barrett, 2011; Goedert et al., 2010; Ronga et al., 2017).³

Two of the included studies had multiple post-adaptation blocks of the landmark task: Schintu et al. (2014) administered nine blocks within 40 minutes after adaptation, and Schintu et al. (2017) had one block immediately after adaptation, with subsequent blocks at 1, 2, 4, 6, and 8 hours. We restricted our analysis to within one hour after adaptation, averaging across all post-adaptation blocks for Schintu et al. (2014), but using only the immediate post-adaptation block for Schintu et al. (2017). Two of the included studies had used sub-group analyses, splitting participants according to the direction of initial bias (Herlihey et al., 2012; Schintu et al., 2017); but we analysed the effect of prism adaptation across all participants, making no distinction according to initial bias (see previous section for rationale). One study using the landmark task had paired peripersonal and extrapersonal space conditions, completed by the same participants around the same period of prism adaptation (Berberovic & Mattingley, 2003). To avoid double-counting these data, we included only the peripersonal condition, as this was more comparable to the other included experiments, which were all conducted within reachable space.

For each experiment, we first extracted, as a raw estimate of effect size, the mean spatial shift following prism adaptation, which we expressed as a percentage of the (average) half length of the stimulus lines in that experiment. For those landmark studies that analysed responses on critical trials only, this raw spatial shift could not be calculated. We also calculated a standardised estimate of statistical effect size (Cohen's d), from the mean and standard deviation of the visuospatial shift after prism adaptation ($d = \text{mean shift}/SD$). For consistency, we used data from prism conditions only, even for three experiments that included a no-prism control, which would enable more *specific* prism effects to be calculated

³ Goedert, Leblanc, Tsai, and Barrett (2010) used a version of line bisection requiring ballistic pointing responses, and also used this bisection task during prism exposure itself. Fortis, Goedert, and Barrett (2011) used the same bisection-based exposure, and studied spatial judgements via an 'incompatible' bisection task with reversed visual feedback. Ronga et al. (2017) used a novel oculomotor adaptation procedure, as well as the traditional pointing method, and a memory-based line bisection task, involving pointing with the eyes closed.

(Guinet & Michel, 2013; Experiments 1 and 2, this paper). If the relevant data were not reported in the original text, we recovered them from figures using an open source plot digitizer⁴ and/or we contacted the corresponding author of the paper. There were two bisection experiments for which the relevant data could not be obtained. In both cases, summary statistics had not been reported in the original paper because the effect of prism adaptation was not significant, and the data were no longer available from the authors (Colent et al., 2000; Michel, Pisella, et al., 2003, Experiment 2). Two non-significant effects are thus missing for the bisection task. Rather than try to impute these values, we will use their known absence to inform discussion.

The major relevant methodological variables, with raw and standardised effect sizes, are listed in Table 1. There was notable variation in the strength of prisms and duration of exposure, and also in the number of trials used for landmark and bisection tasks, which was generally far fewer for bisection (median 10 trials, range 10-90) or landmark tasks using critical trials (median 10, range 10-14), than for landmark tasks using the PSE method (median 78 trials, range 54-550). In total, across 12 sources, there were 17 experiments included for the landmark task (total $n = 256$), and 12 experiments included for line bisection (total $n = 172$) (Table 1).

Raw and standardised effect-sizes

The first step of quantitative analysis was to assess the relation between raw and standardised estimates of effect size. Figure 4a depicts this relationship for the 11 landmark datasets for which a raw spatial measure could be computed (i.e. those that used a PSE analysis). Figure 4b shows the equivalent relationship for the 12 bisection datasets. The raw spatial shift on the landmark task never much exceeded 1% of the line half-length, but for line bisection it ranged up to 4%. For both tasks, there was a strong linear relationship between raw and standardised effect sizes, but the fit was tighter for landmark than for bisection ($r^2 = .85$ vs $.74$). The slope of the relationship was also more than twice as steep for the landmark task (1.0 vs. 0.41), such that a given spatial shift corresponded to a statistically stronger effect. Thus, line bisection performance can show bigger spatial shifts, but the landmark task is a more precise indicator, more consistent across studies, and with a higher signal-to-noise ratio.

⁴ WebPlotDigitizer v4.1, <https://automeris.io/WebPlotDigitizer/>

This may be due, at least in part, to the greater number of trials from which the PSE measure is derived. Regardless of these differences, this first step of analysis gives us confidence, for both tasks, that standardised effect sizes will not misrepresent the patterns for the raw effects.

Meta-analysis

There was considerable methodological variation between studies, most importantly in the prism strength and exposure duration for the adaptation procedure, which might modulate the effective ‘dosage’.⁵ This implies that the size of the true effect was not fixed, but may have varied across studies. We thus performed a random-effects meta-analysis, to estimate the average effect size and its dispersion (Borenstein, Hedges, Higgins, & Rothstein, 2009), using the *metafor* package in R (Viechtbauer, 2010). For each task, an initial random-effects model of standardised effect sizes confirmed substantial heterogeneity between studies ($\tau^2 = 0.19$ and 0.38 for landmark and line bisection respectively). This heterogeneity is illustrated in Figures 4c and 4d, which show funnel plots of effect sizes against standard errors [$1/\sqrt{n}$]. Studies are distinguished according to prism strength and exposure duration (short or long), and the visual patterns suggest that these methodological variables may account for some of the heterogeneity in outcomes. Larger effect sizes tend to follow higher strength prisms, and effect sizes tend to be relatively smaller when the exposure duration is short (< 10 minutes). It is also clear that the larger studies (higher in plot) tend to be the ones that used short exposure durations, presumably for efficiency.

The apparent covariation between study size and exposure duration makes it possible that larger and smaller studies may differ systematically in the true effect sizes studied. Specifically, if short prism exposures induce weaker visuospatial aftereffects, then larger studies may tend to be associated with smaller effects, and smaller studies with larger effects. This is important to note, because an asymmetrical funnel plot showing larger effects for smaller studies can sometimes be taken to suggest publication bias. It may thus be important to take exposure duration into account as a moderator variable, before formally assessing the funnel plots for asymmetry. We chose to encode exposure duration as a dichotomous

⁵ The number of pointing movements made during prism exposure may potentially be more important than the duration *per se*; but this number was not routinely reported across studies (see Table 1). Neither was it possible to analyse the degree of adaptation, in terms of the size of sensorimotor aftereffects, because different studies used different methods to assess these (e.g. open-loop pointing, visual straight-ahead judgements, proprioceptive straight-ahead judgements), or reported only an informal check that adaptation had taken place (Colent et al., 2000; Nijboer et al., 2010).

variable, to capture our impression that exposures of less than ten minutes are unusually short. There are good arguments against the routine dichotomisation of continuous variables (MacCallum, Zhang, Preacher, & Rucker, 2002), but we think it is justified in this case, not least because the continuous index of duration almost certainly has some spurious precision, due to unaccounted uncertainty over the number of pointing movements made in a given duration. The operational distinction between short and long exposures is a pragmatic choice for our analysis, but the possible functional significance of this division will be addressed in subsequent discussion.

We additionally wished to consider a potential moderating role for line length, because it is known that bisection errors increase with line length in patients with neglect (Bisiach, Bulgarelli, Sterzi, & Vallar, 1983; Butter, Mark, & Heilman, 1988; Nichelli, Rinaldi, & Cubelli, 1989), and because Michel et al. (2003, Experiment 2) reported larger visuospatial aftereffects of prism adaptation in their landmark task when longer lines were used. Evaluation of the role of line length was complicated by the fact that different studies presented their stimuli at different viewing distances, between 200 and 600 mm (see Table 1). We therefore wished to encode line length in the distance-independent units of visual angle. However, in four studies using pen-and-paper bisection, no exact viewing distance was specified. For these studies, we imputed a plausible tabletop viewing distance of 375 mm, allowing line length to be recoded into an approximate visual angle for all studies.

An exploratory analysis of correlations with standardised effect size found the highest correlations for prism strength ($r = .67$ for landmark; $r = .58$ for bisection), intermediate correlations for exposure duration ($r = .33$ for landmark; $r = .54$ for bisection), and near-zero correlations for line length ($r = -.07$ for landmark; $r = -.01$ for bisection). We thus used prism strength and exposure duration as moderator variables in our random-effects meta-analyses (Viechtbauer, 2007). For the landmark task, these moderators had a significant omnibus effect [$QM(2) = 14.13$, $p = .0009$], accounting for 57% of the total heterogeneity, leaving moderate residual heterogeneity between studies [$\tau^2 = 0.08$ (SE 0.06); $I^2 = 54\%$; $QE(14) = 30.01$, $p = .008$]. For line bisection, they accounted for 51% of the total heterogeneity [$QM(2) = 10.11$, $p = .006$], leaving high residual heterogeneity [$\tau^2 = 0.19$ (SE 0.13); $I^2 = 71\%$; $QE(9) = 30.65$, $p = .0003$]. Figures 4e and 4f show funnel plots of residual effect sizes, after moderation. The landmark task shows no evidence of asymmetry, but the plot for the bisection task shows a significant asymmetry, such that smaller group studies are associated with larger effects. However, data are known to be missing for two small-group null effects,

which would occupy the lower-left of the plot (see Table 1). These missing data could partly or wholly account for the residual asymmetry. Given this asymmetry, and the missing data, the meta-analytic model for the bisection task should be treated with extra caution.

The parameter estimates and test statistics are given in Table 2. The average influence of prism strength was similar between tasks, with an increase in standardised effect size of 0.11 per degree of prismatic displacement within the studied range (8-17°). A long exposure duration gave an additional boost. Figure 5 shows the predicted average effect size for each task as a function of prism strength, for short (upper plots) and long exposures (lower plots). The shaded grey zone shows the 95% confidence intervals; the average effect can be considered significant where these do not include zero. The dotted lines show the prediction intervals, within which we would expect the true effect size to fall in 95% of individual studies (IntHout, Ioannidis, Rovers, & Goeman, 2016). The prediction is much less precise for line bisection than for the landmark task. This is not just because there were fewer experiments for line bisection, but chiefly because the residual heterogeneity between experiments was higher ($\tau^2 = .19$ vs. $.08$; see Figures 4e and 4f). Further exploration suggests that the precise bisection response method might be important, because omitting from the meta-analysis the one study that used a mouse-guided rather than a direct manual response (Experiment 2, this paper) would almost halve the residual heterogeneity ($\tau^2 = .10$, (SE 0.10); $I^2 = 56\%$; $QE(8) = 17.60$, $p = .025$). The heterogeneity of effects for line bisection will be discussed in due course, but here we will concentrate on the higher-quality model for the landmark task.

According to the left panels of Figure 5, a short period (< 10 mins) of leftward prism adaptation does not induce a significant average shift on the landmark task unless combined with a prism strength greater than 12.5° . With longer exposure durations, the visuospatial effects are boosted, so that a significant average shift is predicted for 10° prisms [$d = 0.42$, 95% CIs 0.11 to 0.72], though the true shift could still be negative in isolated studies (lower bound 95% prediction interval -0.22). At a prism strength of 15° , a very large average effect is predicted [$d = 0.94$, 95% CIs 0.64 to 1.24], and negative shifts should never arise (lower bound 95% prediction interval 0.31). Referring back to the equation in Figure 4a, our corresponding estimate for the average raw spatial shift in PSE after a long period of adaptation to 15° prisms is 0.81% of stimulus half-length (95% CIs 0.51 to 1.11).

11. General discussion

We have reported two historical experiments that failed to find any trace of visuospatial aftereffects of leftward prism adaptation in healthy young adults. These null results puzzled us privately for some time; but a weighted consideration of our data, with the accumulated evidence in the literature, shows that they fit coherently into the broader pattern. This broader pattern confirms systematic visuospatial aftereffects of prism adaptation, and highlights methodological factors that influence the likelihood of detecting them. Our failures to replicate do not challenge other evidence; rather, they can be combined with it to refine our understanding of the phenomenon of interest.

The major procedural factor influencing the detectability of visuospatial aftereffects is the strength of the prisms to which participants are adapted. This may seem obvious, but only recently has there been any attempt to study the effect of prism power experimentally (Michel & Cruz, 2015; Striemer et al., 2016). Michel & Cruz (2015) adapted three groups of eight participants to different shifts (8° , 10° , 15°), using a 20 minute exposure, and measured the effects on line bisection and landmark tasks (see Table 1). They concluded that 8° prisms are insufficient to induce visuospatial aftereffects, that 10° prisms can cause a shift in manual bisection but not the landmark task, and that 15° prisms can cause a shift in either task. Our meta-analysis, to which their data contribute, suggests that their specific results can be understood as stochastic reflections of the effect sizes associated with leftward prisms of different strength (Figure 5). For a long exposure duration, the average visuospatial effect size associated with 8° prisms does not differ significantly from zero for either task, while at 10° the average effect is more detectable for line bisection than for landmark ($d = 0.64$ vs 0.43), and at 15° it is highly detectable for either task ($d = 1.18$ and 0.95). The actual effect observed in a given experiment may depend on additional procedural factors, as yet uncharted, and also on chance sampling variation.

Of course, whether a given effect is likely to be judged as significant in a given study depends critically upon the sample size. Sample sizes in this literature have been small-to-modest ($n = 7$ -40), so we should expect patterns of significance to vary. For instance, in contrast to Michel & Cruz (2015), Striemer and colleagues (2016) found that adaptation to 8.5° prisms induced a significant shift in landmark judgements but not line bisection, whereas Striemer & Danckert (2010) found significant aftereffects of 10° prisms on both tasks, and we found null effects of 10° prisms on landmark judgements and of 12° prisms on line

bisection. Similarly, Schintu et al. (2014) reported that the perceptual aftereffects of prism adaptation were significant in some post-prism blocks, but not in others. Fluctuating significance is what we would expect in any series of measures of an effect, even if the effect itself is constant, so we should perhaps not put too much theoretical weight on specific patterns of significance in individual studies. A meta-analytic approach helps us to see the bigger picture. This picture is more blurred for line bisection than for landmark, but there is a clear and congruent dose-response relationship between prism strength and visuospatial aftereffects.

This dose-response relationship is strong evidence that the visuospatial shifts are true consequences of prism adaptation, and not due to some other factor, such as declining alertness over a long testing session. It is arguably the only strong evidence for this conclusion, as most of the studies in this area have been conducted without controls for general factors such as alertness. As noted in Section 2, four studies did use both leftward and rightward prisms, but did not test directly for a difference between these conditions (Berberovic & Mattingley, 2003; Colent et al., 2000; Schintu et al., 2014, 2017). Examination of the data from those papers suggests that the critical differences would not have reached significance if they had been tested. Moreover, Berberovic & Mattingley (2003) reported a significant rightward shift of landmark judgements in extrapersonal space, for leftward and rightward prisms alike. Only one experiment, other than those in the present paper, has included a no-prism control condition (Guinet & Michel, 2013). This experiment did show a rightward shift after prism adaptation that was significant by comparison with the control group. But the task used was manual line bisection, so the shift could in principle have been due to a sensorimotor aftereffect, rather than a change in visuospatial perception (see later discussion of bisection task).

Our meta-analysis secondly suggested a dose-response relationship by exposure duration. We operationally divided studies into short (< 10 minutes) and long (10 minutes +) exposures, and found that effect sizes were boosted for long exposures. We chose exposure duration as a moderator variable, because this information was available across all studies, but the more critical moderator seems likely to be the number of pointing movements made. Spatial errors are usually eliminated within 30 trials of exposure, but continued exposure beyond this point induces deeper, consolidated adaptation. In a single-case monkey study, Yin and Kitazawa (2001) found that the sensorimotor aftereffects of 250 or fewer exposure trials were not visible at 24 hours, but that 500 trials of exposure induced aftereffects for up

to three days. In humans, the immediate rate of decay of sensorimotor aftereffects after a 500-trial exposure is half of that found after a 150 trial exposure, with greater retention at 24 hours (Inoue et al., 2015). These patterns have been taken to suggest that an ‘ultraslow’ process, responsible for consolidated adaptation, may become active after around 250 exposure trials (Inoue et al., 2015). Our distinction between short and long exposure might reflect the differential engagement of this ultraslow system.

The third major factor accounting for differences in visuospatial aftereffects was the probe task itself. Line bisection was associated with larger spatial shifts (Figures 4a-b), yet had a weaker signal-to-noise ratio in terms of standardised effect, perhaps due to the smaller number of trials typical for this method and/or to added variability associated with manual responding. Prism effects were also more heterogeneous for line bisection than for landmark studies (Figures 4e-f), so the effect size estimates were less precise, even if the *average* effect was larger (Figure 5). We did not formally compare landmark studies that used the PSE method with those that relied on critical trials, but the latter method uses many fewer trials and seems *a priori* less stable. For instance, a small change in visuospatial bias, which shifts the PSE by a fraction of a millimetre, could reverse all of a person’s responses on critical trials, or leave them unchanged, depending on how their prior PSE was poised. The critical trials method may be useful when it is possible to collect a few trials only, but the PSE method of the landmark task seems to be the best standard probe for the visuospatial aftereffects of prism adaptation.

So what is the problem with line bisection? As discussed in Section 6, two major factors may compromise its utility in this context. The first is that the manual response is prone to contamination from sensorimotor aftereffects. Researchers may try to limit this by asking for slow deliberate responses, with small movements made under visual control, but if people respect these instructions to differing degrees, and if different studies emphasise them differently, then we might expect an overall larger spatial shift, but with added variability between participants (lowering the signal-to-noise ratio), and between studies (increasing heterogeneity). In Experiment 2, we tried to avoid any direct influence of sensorimotor aftereffects, by using a mouse-controlled bisection task, in which the hand is hidden from view, and a visible cursor is controlled in screen-relative coordinates. We saw no shift in DBE, despite robust sensorimotor aftereffects, suggesting that this indirect response did avoid contamination. This experiment was influential in our meta-analysis of bisection studies,

accounting for around half of the residual heterogeneity, consistent with an important role for the bisection response method.

The second factor is that the traditional measure of DBE is not the best measure of bias on the bisection task. An alternative, endpoint weightings analysis yields a measure (EWB) that is more sensitive to the pathological bias of neglect and also to the subtle pseudoneglect of healthy people (McIntosh, 2006, 2017, McIntosh et al., 2017, 2005b). This was evident in Experiment 2, in which DBE showed a non-significant pseudoneglect, with moderate effect size ($d = -0.27$), whilst the pseudoneglect revealed by EWB *in the same bisection data* was very robust ($d = -0.95$). On this basis, we suggest that the endpoint weightings analysis will likewise be more sensitive to a prism-induced visuospatial shift. It should also be largely or wholly immune to sensorimotor aftereffects, because the endpoint weightings are extracted from the pattern of change in responses across stimuli, so should be unaffected by any constant shift in response position. Studies seeking to measure the effect of prisms on line bisection might therefore adopt methods similar to those of our Experiment 2, for the same reasons that we did. At present, the relevant data from traditional manual methods of line bisection are somewhat noisy and ambiguous.

12. Conclusion

The visuospatial aftereffects of leftward prism adaptation are real and robust. To harness them, we recommend that researchers should expose participants to 15° (or higher) prisms for more than ten minutes, with upwards of 250 pointing movements. Power calculations for the required sample size should take account of heterogeneity in the true effect between studies; and further research into the procedural factors underlying this heterogeneity will help to refine optimally-effective methods. Adequately-powered studies should compare the effects of leftward and rightward adaptation, and distinguish these from more general effects of alertness. Moreover, prior suggestions that the effects of prism adaptation depend upon the pre-existing visuospatial bias should be tested using designs that rule out regression artefacts. We suggest that researchers should avoid the traditional format of the line bisection task, because direct manual responses may be contaminated by sensorimotor aftereffects of prisms. A more sensitive and valid probe is the psychophysical estimation of PSE in the landmark task. The visuospatial shifts induced may be tiny, at less than one percent of stimulus half-length, but their implications could have a far longer reach.

This paper is concerned with two specific visuospatial tasks, but the effects of prisms have been explored across a wide range of attentional (e.g. Bultitude, List, & Aimola Davies, 2013; Bultitude & Woods, 2010; Morris et al., 2004), representational (Loftus et al., 2008; Nicholls & Loftus, 2007), non-visual (e.g. Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004; Michel, Rossetti, Rode, & Tilikete, 2003), and other tasks (see Michel, 2016, for a review). An extension of the meta-analytic approach to this broader range of contexts might bring more order to the sometimes-confusing mix of positive and null results, and help to relate the behavioural findings to changes in neural activations within attentional networks (Clarke & Crottaz-Herbette, 2016; Crottaz-Herbette, Fornari, Tissieres, & Clarke, 2017). A quantitative overview of the effects of this treatment in the healthy brain, and the influence of methodological factors, including prism direction, would deepen our understanding of the relation between sensorimotor alignment and spatial cognition. It could also accelerate the development of more effective therapies for spatial neglect and other disabling disorders.

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Source			Prism exposure method			Landmark task			Line bisection		
1 st author (year)	Experiment	n	Prism°	Duration (mins)	No. of movements	No.*length (distance)	Analysis	Effect size	No.*length (distance)	Method	Effect size
Colent (2000)	1	7	15	20	unspecified	78*250mm (unspecified)	PSE	raw 0.89% d = 1.36	10*250mm (unspecified)	pen/paper	NULL
Michel (2003)	1 (mid-space)	10	15	20	unspecified	105*250mm (450 mm)	PSE	raw 0.56% d = 0.74	18*250mm (450 mm)	pen/paper	raw 1.68% d = 1.11
	2 (average)	7	15	20	unspecified	35*125mm 35*250mm 35*375mm (450 mm)	PSE	raw 0.56% d = 0.71	6*125mm 6*250mm 6*375mm (450 mm)	pen/paper	NULL
	3 (active)	10	15	20	unspecified	78*250mm (450 mm)	PSE	raw 0.88% d = 1.16	10*250mm (450 mm)	pen/paper	raw 1.92% d = 0.63
Berberovic (2003)	1 (peripersonal)	16	10	15-20	200	234*172mm (500 mm)	PSE	raw 0.10% d = 0.52			
Nijboer (2010)	1	15	15	10	unspecified	14*250mm (350 mm)	Critical	raw NA d=1.68			
Strierner (2010)	1	8	10	10	200-300	10*200mm (unspecified)	Critical	raw NA d=0.41	10*236mm (unspecified)	pen/paper	raw 1.39% d = 1.24
Herlihey (2012)	1 (concurrent)	20	10	6.8	204	10*187mm (200 mm)	Critical	raw NA d = 0.00	10*187mm (200 mm)	touch stylus	raw 0.24% d = 0.35
	1 (terminal)	20	10	6.8	204	10*187mm (200 mm)	Critical	raw NA d = 0.26	10*187mm (200 mm)	pen/paper	raw -0.01% d = 0.01
Guinet (2013)	1 (prism group)	9	15	15	540				10*250mm (400 mm)	pen/paper	raw 2.89% d = 2.11
Schintu (2014)	1	20	15	5-7	150	66*350mm (350 mm)	PSE	raw 0.65% d = 0.72			
	1	8	8	20	360	54*250mm	PSE	raw -0.57%	10*250mm	pen/paper	raw 0.10%

Michel (2015)						(450 mm)		d = -0.43	(450 mm)		d = 0.05
	1	8	10	20	360	54*250mm (450 mm)	PSE	raw 0.26% d = 0.26	10*250mm (450 mm)	pen/paper	raw 1.98% d = 0.89
	1	8	15	20	360	54*250mm (450 mm)	PSE	raw 1.14% d = 0.92	10*250mm (450 mm)	pen/paper	raw 4.60% d = 1.54
Strierner (2016)	1	22	8.5	7-10	200	10*200mm (unspecified)	Critical	raw NA d = 0.27	10*200mm (unspecified)	pen/paper	raw -0.32% d = -0.16
		25	17	7-10	200	10*200mm (unspecified)	Critical	raw NA d = 0.44	10*200mm (unspecified)	pen/paper	raw 1.15% d = 0.61
Schintu et al, 2017	1 (early post- test)	40	15	5-7	150	66*350mm (350 mm)	PSE	raw 0.20% d = 0.13			
McIntosh (2018)	1	12	10	20	635 (average)	550*300mm (500 mm)	PSE	raw -0.02% d = 0.02			
	2 (single & multi-step)	24	12	10	120				90*160mm average (600 mm)	occluded mouse	raw 0.02% d = 0.14

Table 1. Key methodological details and estimated effect sizes for the leftward-prism adaptation datasets in the meta-analysis. Shaded cells show where a task was not part of a given study. NULL indicates that the data needed to calculate effect sizes for a reported null effect were not available.

	Coefficient	SE	95% CIs	z test
Landmark task				
Intercept	-1.04	0.44	[-1.90, -0.17]	$z = -2.35, p = .019$
Prism strength	0.11	0.03	[0.04, 0.17]	$z = 3.20, p = .001$
Exposure (long)	0.40	0.19	[0.02, 0.78]	$z = 2.07, p = .038$
Line bisection				
Intercept	-1.03	0.63	[-2.26, 0.21]	$z = -1.62, p = .104$
Prism strength	0.11	0.05	[0.01, 0.21]	$z = 2.10, p = .036$
Exposure (long)	0.61	0.31	[0.00, 1.22]	$z = 1.96, p = .050$

Table 2. Parameters and test statistics for random-effects meta-analyses for landmark task and line bisection, with prism strength and exposure duration (short vs long) as moderators.

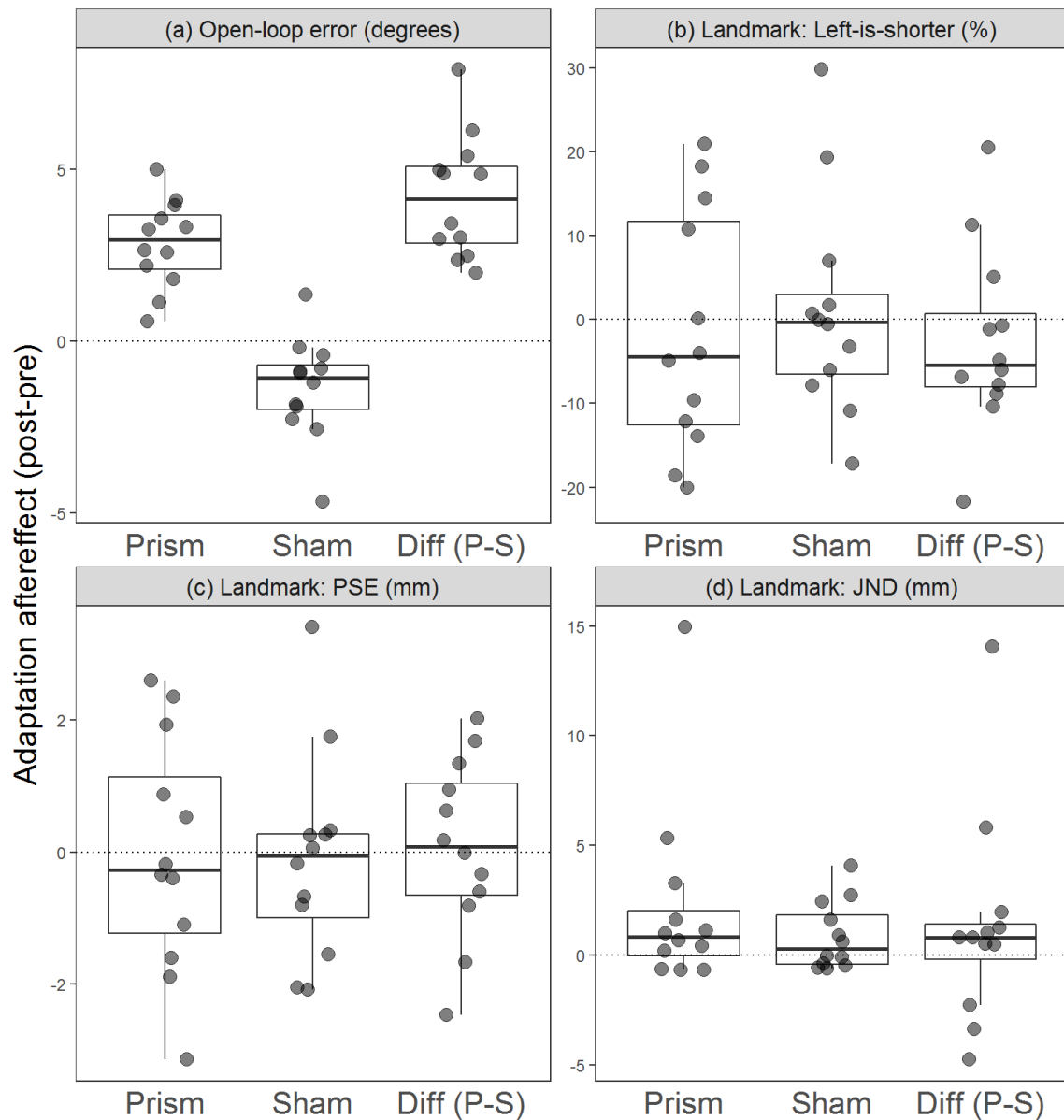


Figure 1. Experiment 1. Post-pre adaptation change by condition (Prism and Sham), and the difference in change between conditions (Prism – Sham) for: **(a)** Open-loop pointing error, encoding the sensorimotor aftereffect; **(b)** Percentage of ‘left-is-shorter’ responses on critical (equal) trials of the landmark task; **(c)** Point of subjective equality (PSE, measure of perceptual bias) in the landmark task; **(d)** Just noticeable difference (JND, measure of perceptual sensitivity) in the landmark task.

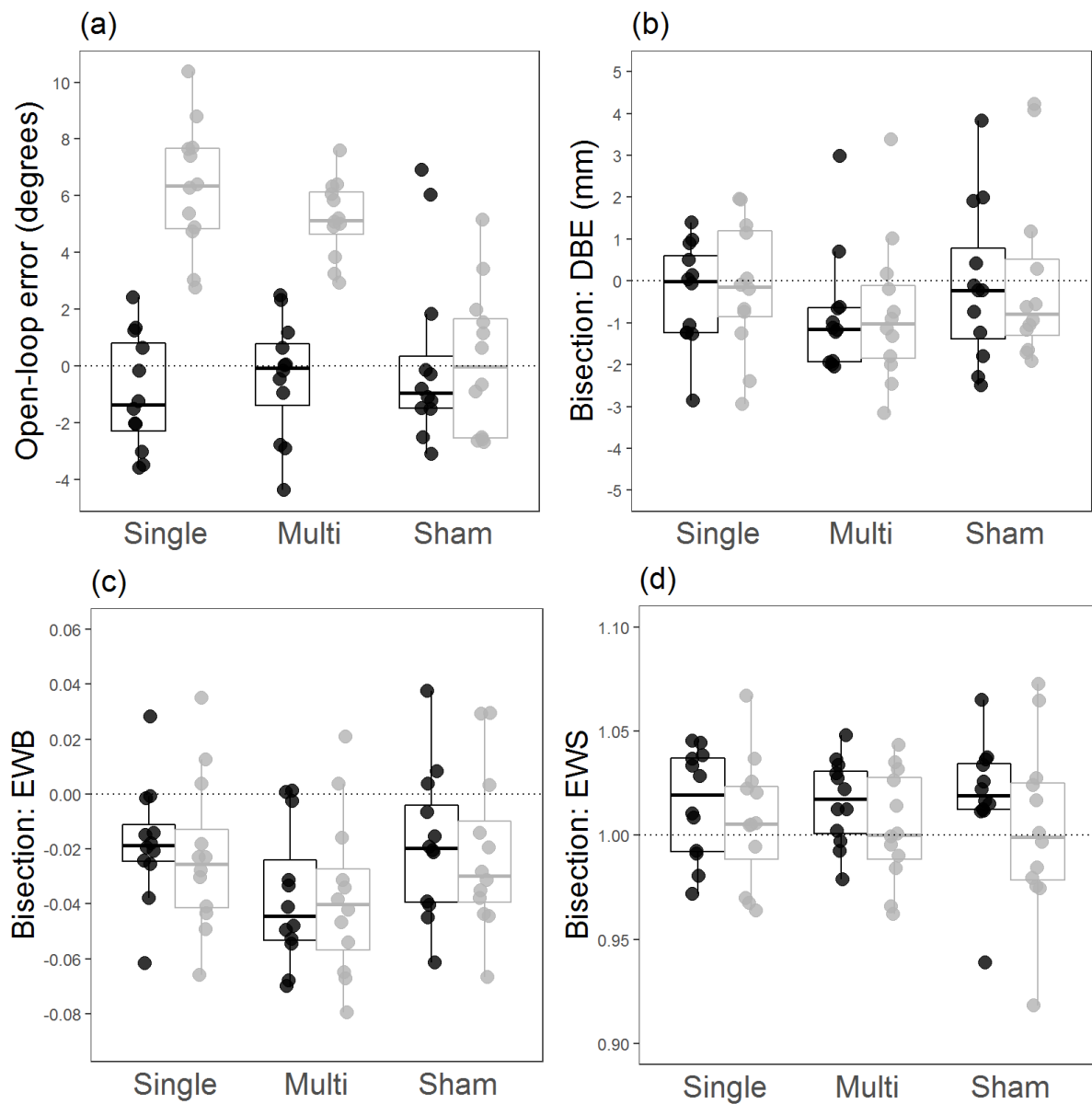


Figure 2. Experiment 2. Pre-adaptation (black plots) and post-adaptation (grey plots) scores by adaptation condition (Single-prism, Multi-prism, Sham) for: **(a)** Open-loop pointing error; **(b)** Directional bisection error; **(c)** Endpoint weightings bias (EWB); **(d)** Endpoint weightings sum (EWS).

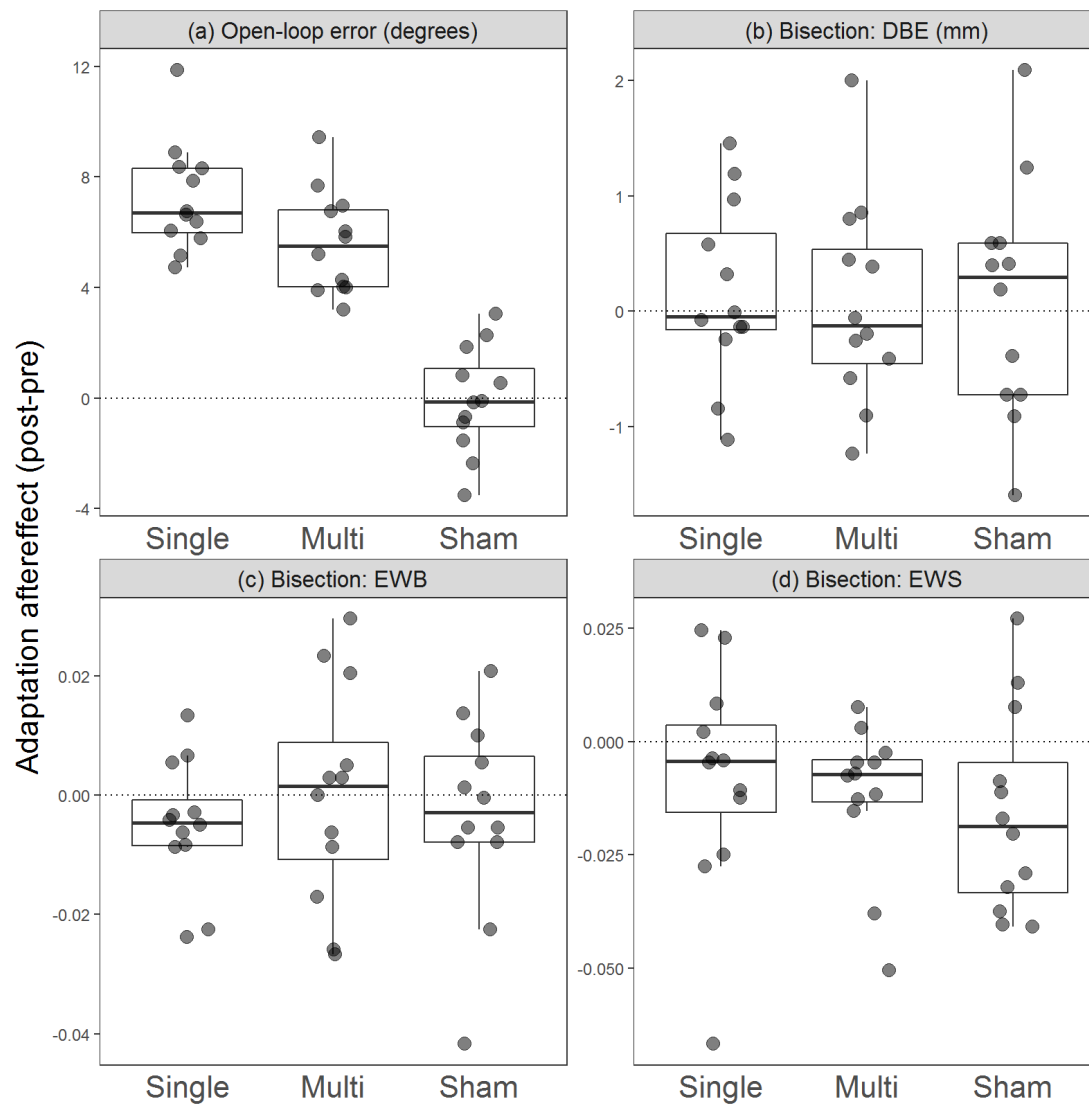


Figure 3. Experiment 2. Post-pre adaptation change by adaptation condition (Single-prism, Multi-prism, Sham) for: **(a)** Open-loop pointing error, encoding sensorimotor aftereffect; **(b)** Directional bisection error; **(c)** Endpoint weightings bias (EWB); **(d)** Endpoint weightings sum (EWS).

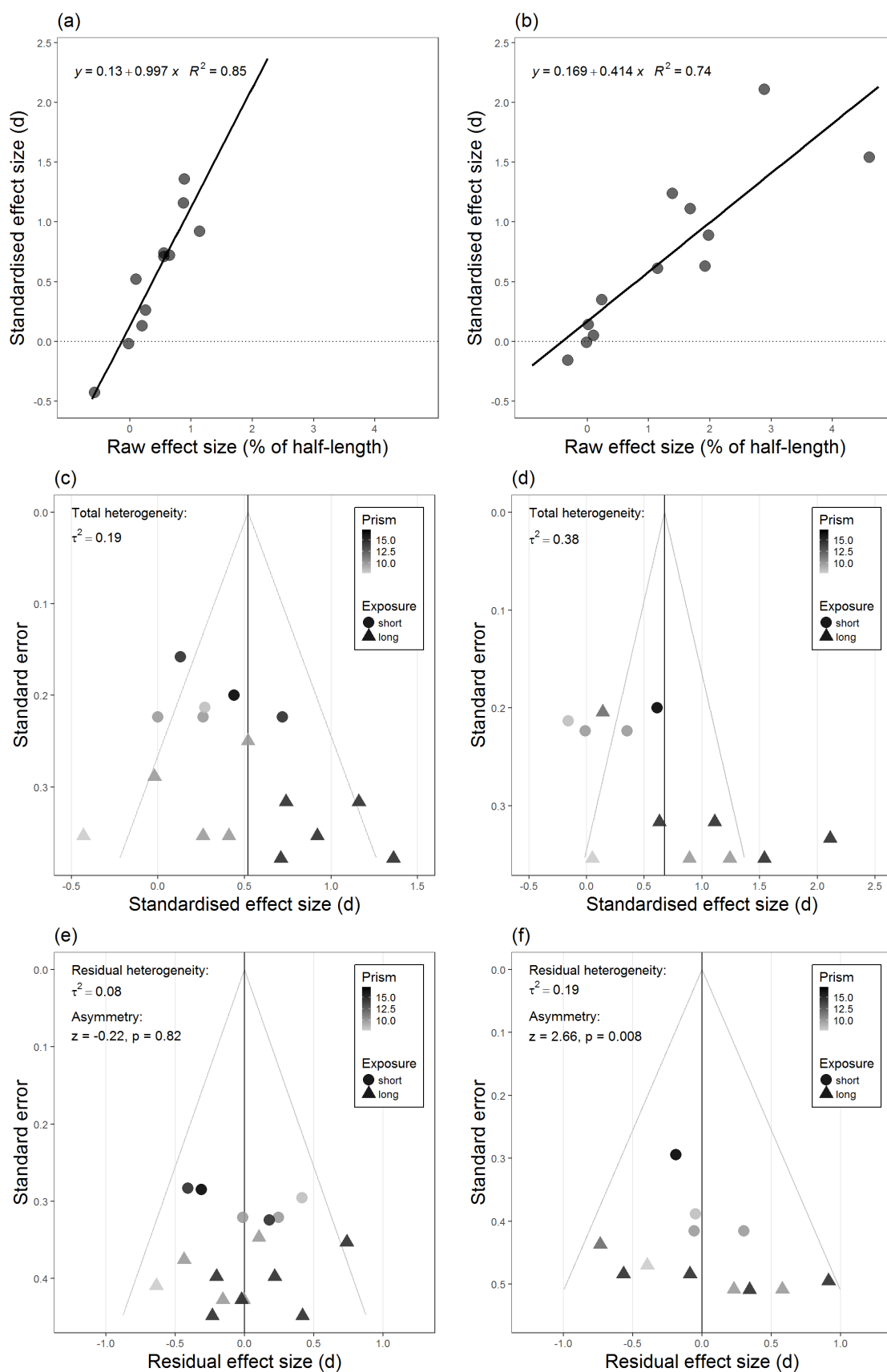


Figure 4. The plots on the left and right show equivalent analyses for landmark and line bisection studies respectively. The top row shows raw spatial vs. standardised effect size for

(a) landmark and **(b)** bisection. The middle row shows unmoderated random-effects funnel plots of standardised effect size by standard error (i.e. larger studies are higher in plot) for **(c)** landmark and **(d)** bisection. Oblique lines indicate the 95% confidence region at each level of standard error, and is centred on the meta-estimate of average effect size according to the random-effects model. For both tasks, some heterogeneity in effect size is systematically related to prism strength and exposure duration. The bottom row shows funnel plots of residual effect size, after moderation by prism strength and exposure duration, for **(e)** landmark and **(f)** bisection. Egger's test of funnel plot asymmetry is significant for line bisection (f), so meta-analytic results for this task should be treated with caution (see text).

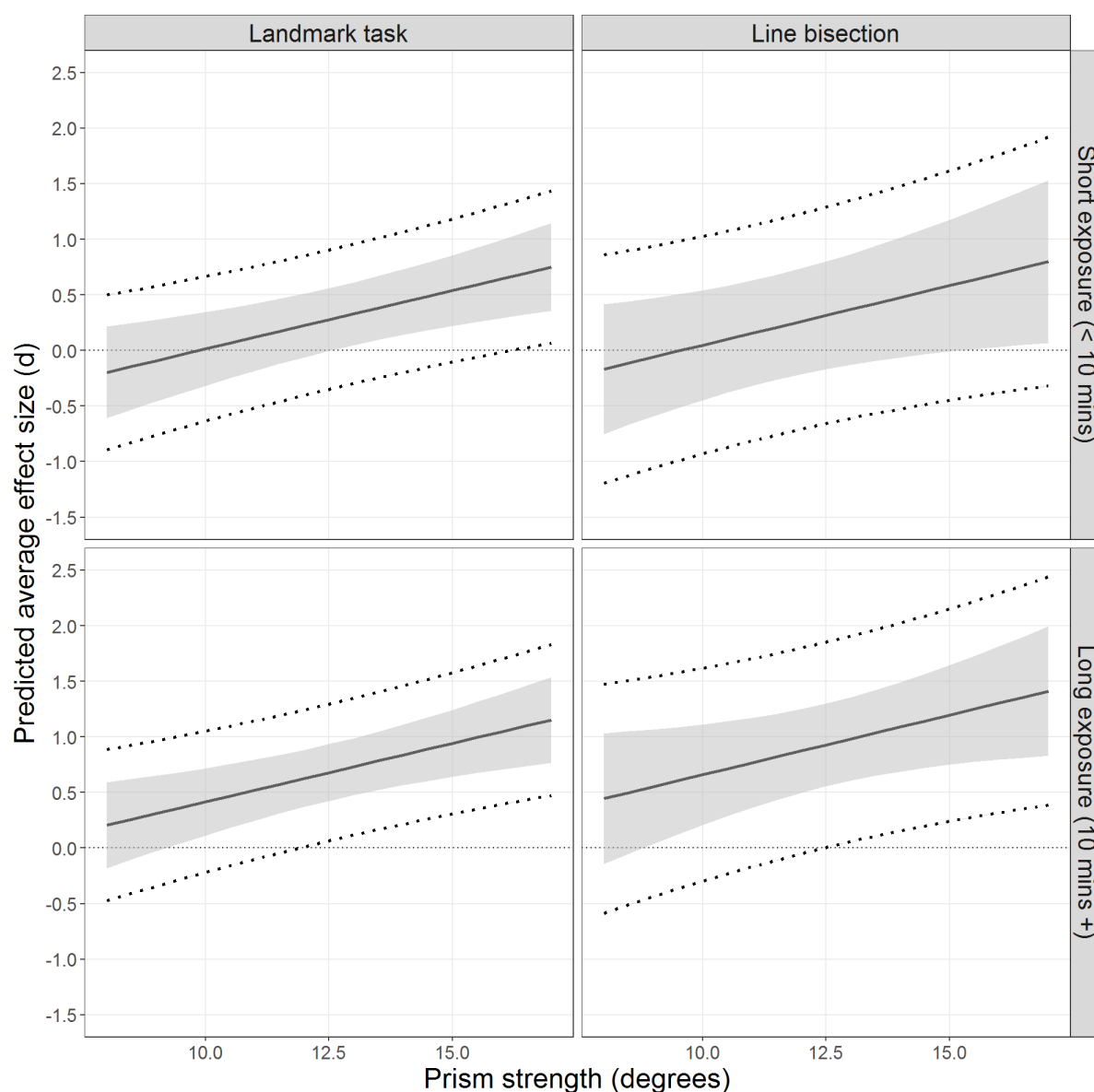


Figure 5. Summary of meta-analysis models, showing predicted average effect size by prism strength (8-17°) and exposure duration (short or long). The grey shaded region shows the 95% confidence intervals, and the dotted lines show the 95% prediction intervals (see text).