Effects of prismatic adaptation on judgements of spatial extent in peripersonal and extrapersonal space

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Abstract

Recent research has shown that visuomotor adaptation to a lateral displacement of the visual field induces significant perceptual aftereffects in normal observers, and in right hemisphere patients with spatial neglect [Neuroreport 11 (2000) 1899; Nature 395 (1998) 166]. These findings suggest that adaptive realignment following prism exposure induces a bias in visual space perception, even in tasks that require no visually guided motor response. Given recent neurophysiological and behavioural data suggesting independent visual representations for peripersonal and extrapersonal space, here we asked whether adaptive aftereffects extend beyond participants’ immediate reaching space to stimuli presented beyond arms’ reach (i.e. in extrapersonal space). Thirty-two participants underwent adaptive realignment to 10° left- or right-deviating wedge-prisms. Before and after adaptation participants performed a visual landmark task that required estimation of the midpoint of horizontal line stimuli. There was a significant rightward shift in visual midpoint judgements following adaptation to left-deviating prisms, which was evident in both peripersonal and extrapersonal space. Paradoxically, a significant rightward shift also occurred following adaptation to right-deviating prisms, but only in extrapersonal space. We suggest that the pattern of adaptive aftereffects observed reflects the different reference frames used by participants to perform spatial judgements in peripersonal and extrapersonal space. We also propose that an underlying hemispheric asymmetry in the processing of spatial errors during adaptation may contribute to the direction of aftereffects in both normal observers, and in patients with unilateral lesions.

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1. Introduction

The effects of sensorimotor adaptation to optical-wedge prisms have been studied in humans for over 100 years [12,32]; for review see [26]. In the standard experimental paradigm, normal observers exposed to a prism-induced displacement of the visual field adapt rapidly by adjusting their motor behaviour (e.g. manual pointing) to reduce errors. With practice there is gradual recalibration of visual and proprioceptive/kinesthetic correspondences, so that motor errors are effectively eliminated [26]. That this adaptation reflects genuine spatial realignment, rather than a conscious strategy adopted by the subject, is supported by the presence of negative aftereffects following removal of the prisms [26,30,37,39].

Although there have been many studies of the behavioural and cognitive effects of prismatic adaptation, the neural basis for these effects has remained uncertain. A recent human neuroimaging study by Clower et al. [1] found significant activity in the posterior parietal cortex contralateral to the reaching limb, during visually guided pointing under conditions of prismatic displacement. Unfortunately, since the direction of prismatic displacement (left versus right) was alternated after every four reaching movements, true adaptive realignment was not achieved. Nevertheless, the results of this pioneering study suggest that the human parietal cortex plays an important role in the detection and correction of spatial errors during manual actions.

More recently, in a series of elegant studies Rossetti and co-workers [29,31,34] have shown that spatial realignment following adaptation to a right-lateral shift of the visual field leads to profound and enduring improvements in patients with spatial neglect due to right hemisphere damage. For instance, Rossetti and co-workers [31] reported that a short (<10 min) period of adaptation to a 10° rightward displacement of the visual field significantly improved the performance of right hemisphere patients on a range of clinical tests for neglect, including line bisection, cancellation, copying, drawing, and reading. Importantly, there was no significant effect of adaptation to leftward displacing prisms, suggesting that the beneficial effects of rightward...
and may even extend over several days [24], thus making prismatic adaptation a useful tool for rehabilitation. These results in neglect patients prompted Colent et al. [2] to examine the effects of prismatic adaptation on visual perception in normals. They compared bisection errors made by normal participants in a standard, manual version of the horizontal line bisection test, and in a ‘landmark’ variant of the task [10]. Following a short period of visuomotor adaptation to 15° left-deviating prisms, normal participants showed a significant rightward deviation in the perceived midpoint of the pretransected lines, relative to a pre-adaptation baseline. Interestingly, this effect was not apparent for the manual version of the test, and did not occur following equivalent adaptation to right-deviating prisms. Thus, adaptation to left-deviating prisms induces rightward ‘pseudoneglect’ in normals [2], but has no effect on pathological neglect in right hemisphere patients. Conversely, adaptation to right-deviating prisms has no effect on bisection judgements in normals, but induces significant and long-lasting improvements in spatial neglect in patients [24,31]. It therefore appears that the processes involved in visuomotor adaptation engage the two hemispheres differentially according to the direction of prism-induced displacement; and that these processes may be differentially susceptible to the effects of lateralised brain damage [31].

In the present study, we attempted to replicate the findings of Colent et al. [2], with several important extensions to their methodology. First, we asked whether the effects of prismatic adaptation on bisection judgements in the landmark task also extend to stimuli presented beyond participants’ immediate reaching space. There is considerable neurophysiological and behavioural evidence in monkey and man that the space within arms’ reach (i.e. ‘peripersonal space’) is represented by neural circuits that are functionally distinct from those devoted to the representation of space beyond arms’ reach (i.e. ‘extrapersonal space’) [25]. Moreover, it is known that visual neglect may occur predominantly in either peripersonal or extrapersonal space, depending presumably on the locus of damage [4,9]. Peripersonal space is typically conceptualised as an ‘action space’, for which visual representations are encoded in body- or limb-centred co-ordinates [25]. In contrast, extrapersonal space is more important for object recognition and visual search, and is probably represented in allocentric or gravitational co-ordinates [25].

Given the results of Colent et al. [2], it is important to determine whether any aftereffects of prismatic adaptation are restricted to perceptual representations of peripersonal space (within which visuomotor adaptation takes place), or whether they extend to perceptual representations of extrapersonal space. In a study of prism adaptation in normals, Tietz and Gogel [33] compared the magnitude of adaptive aftereffects induced by manual pointing toward visual targets projected at two different depths (33.0 cm versus 55.9 cm). They observed significant generalisation of aftereffects across the two depths, the magnitude of which depended on whether the space between the participant and the targets was visible. Note however that the targets in this study were always within reaching distance (participants used a pen to mark their locations on a board), and so the results do not indicate whether adaptive aftereffects extend into extrapersonal space. The first aim of the present study, therefore, was to determine whether the visual aftereffects of prismatic adaptation, as measured by the landmark task, occur in extrapersonal space as well as in peripersonal space.

A second aim of this study was to determine whether prismatic aftereffects result directly from an egocentric bias in judgements of the subjective midline. In the study by Colent et al. [2], horizontal lines were always centred on the participants’ body midline. Thus, the rightward bias in landmark judgements found after adaptation to left-deviating prisms may have been due to a shift in participants’ egocentric midline, rather than to a bias in the allocentric representation of the lines themselves. To address this issue, we presented line stimuli so that they were either aligned with the participants’ body midline, or displaced horizontally toward the left or right hemisphere. We also measured participants’ perception of their egocentric midline by having them point straight-ahead, without visual guidance, before and after prismatic adaptation. This permitted us to compare individuals’ egocentric judgements of straighthead with their allocentric judgements on the landmark stimuli.

Finally, in order to avoid any unwanted influences from extraneous marks or distractions in the environment, we projected the lines onto a white viewing screen in an otherwise darkened room. By moving the participant and projector between blocks, we were also able to ensure that the landmark stimuli were precisely matched for retinal angle across peripersonal and extrapersonal space conditions.

2. Method

2.1. Participants

Thirty-two undergraduate students (12 males 20 females; age range 18–35 years) from the University of Melbourne participated for course credit. All participants were right-handed and had normal or corrected-to-normal vision.
2.2. Apparatus and stimuli

2.2.1. Prismatic adaptation

Participants wore a pair of CebeTMS binocular prisms to induce a left- or right-lateral displacement of the visual field. Each circular eyepiece contained a clear wedge prism that displaced the visual field horizontally by 10° to the left or right. Black leather covers attached to the temporal and nasal portions of the frames ensured that participants could not see any undistorted portions of the visual field peripherally.

A wooden adaptation box (330 mm high × 920 mm wide × 910 mm long) was constructed, based upon the design of Rossetti and co-workers [31]; see Fig. 1. The base of the box was lined with black, carbon-impregnated paper (800 mm × 800 mm), which permitted an electrical current to be passed across it, thus providing a means of measuring the spatial position of participants’ pointing responses pre- and post-adaptation. The sensitive surface of the box was calibrated prior to testing, and had a spatial accuracy of ±1.3 mm. The box was painted matte black to remove extraneous landmarks and any reflective surfaces.

The box was open at the top to allow participants to view visual targets marked on the sensitive surface, and to observe their own pointing movements. A black occluding board was positioned immediately below each participant’s chin, across the open top of the box, in order to obscure their view of the starting position of their hand. There were four boards that varied in width (110, 170, 200 and 300 mm) to accommodate the different heights of participants.

Two faint diagonal lines were drawn on the surface of the box, extending at a 10° angle to the left and right from a common central position aligned with participants’ mid-sagittal axis. These lines were used as visual targets for participants’ pointing movements during prismatic adaptation. Participants wore a metal thimble on the index finger of their preferred (right) hand. The thimble and the active surface of the box were connected to a liquid crystal display (LCD), which provided a digital readout of the endpoint of participants’ pointing responses.

2.2.2. Landmark task

Horizontal lines were generated individually on a Pentium II PC (Toshiba Tecra Model 530 CDT) and projected onto a white screen (1200 mm wide × 903 mm high) via an LCD data projector (Panasonic Model PTL 566). Line stimuli appeared white against a uniform black background.

Participants viewed the displays from each of two distances: (1) peripersonal space (50 cm); and (2) extrapersonal space (116 cm). The size of line stimuli was adjusted across viewing distances to ensure the horizontal retinal angle subtended remained constant at 19.03°. Line stimuli appeared either centrally on the screen, or displaced slightly to the left or right by 3.16°. Transection marks were 1.52° in vertical length and 0.08° thick. There were six transection offsets (in one pixel increments) on either side of the midpoint of the horizontal line, in addition to a zero offset (correct bisection). The visual angle of a single pixel was 0.04°. There were six lines for each transection offset at each spatial location (left, centre, right), yielding a total of 234 stimuli. A button-box was interfaced with the computer via the serial port, and was used by participants to indicate whether the line stimuli were transected to the left or right of centre.

2.3. Procedure

All data were collected in a darkened room free from noise and other distractions. Each participant individually completed the following sequence of tests: (1) pre-adaptation open-loop test; (2) pre-adaptation landmark task; (3) visuomotor adaptation to left- or right-prismatic deviation; (4) post-adaptation open-loop test; (5) post-adaptation landmark task. Sixteen participants were adapted to a left-lateral shift of the visual field, and a further 16 were adapted to a right-lateral shift. Within each group half of the participants...
used their left hand for adaptation and open-loop pointing tests, and half used their right hand.

2.3.1. Pre-adaptation landmark task
Participants were seated directly in front of the display screen, with room lights extinguished to reduce external visual cues. Each line was presented for a maximum of 5 s (or until a response was made), and was followed by a black and white pattern mask which remained visible for 2 s before the next stimulus line was displayed. Participants were instructed to indicate whether the vertical transection mark was located closer to the left or right end of the horizontal line by making one of two bimanual button-presses. For lines transected to the left of the midpoint they used their left-middle and right-index fingers, whereas for lines transected to the right they used their right-middle and left-index fingers. Bimanual responses were used to avoid any asymmetry in hemispheric activation that may be associated with unimanual or verbal responses [14,15]. No feedback concerning accuracy was provided.

Line stimuli were presented in random order in two blocks of 234 trials, one for each viewing distance. Each block took approximately 10–15 min to complete. The order of testing in peripersonal and extrapersonal space was counterbalanced across participants. Accuracy and response times were recorded automatically by the computer for each display, and stored for later analysis.

2.3.2. Pre-adaptation open-loop pointing
In order to determine the effect of prismatic adaptation on egocentric judgements of straight-ahead, participants completed an open-loop pointing test before and after adaptation. Participants were seated in front of the adaptation box, with their head and body aligned with its centre. With their vision occluded, participants were required to point straight ahead, i.e. in alignment with their mid-sagittal axis, onto the sensitive surface of the box. The spatial position of the endpoint of each movement was displayed on the LCD readout, and recorded manually by an experimenter. Following each response participants were instructed to return their hand to a starting pad located immediately beneath their chin. There were 10 trials in total, and participants were not given feedback on the accuracy of their responses.

2.3.3. Visuomotor adaptation
Immediately following the pre-adaptation open-loop pointing, participants put on the optical prisms and were asked to point to the left- and right-sided targets as quickly and as accurately as possible. The experimenter instructed participants verbally on which target to point to prior to each trial, according to a random sequence. After each pointing movement, the experimenter recorded the terminal position of the index finger and instructed participants to return their hand to the pad beneath their chin. Starting position of the hand was occluded to ensure effective adaptation [26].

Accuracy of pointing was recorded for the first 50 movements. This provided a profile of the direct effects of prismatic displacement, which reflect trial by trial error correction [26]. Participants then continued pointing to left and right targets as instructed for a further 150 movements. The last 150 movements were not recorded for accuracy, as participants typically reached an asymptote of pointing accuracy within the first 50 trials. The adaptation procedure took approximately 15–20 min to complete.

2.3.4. Post-adaptation open-loop test
Immediately following adaptation the prisms were removed and participants were blindfolded to reduce any spontaneous de-adaptation. They were then required to point 10 times straight ahead (as in the pre-adaptation phase) without visual feedback, in order to measure the extent of any prism-induced aftereffect on proprioceptive judgements of the egocentric midline.

2.3.5. Post-adaptation landmark task
The landmark task was repeated, following the same procedure as that described for the pre-adaptation phase. The order of presentation in peripersonal and extrapersonal space was again counterbalanced across participants, and lines at different positions were presented to each participant in random order.

3. Results
For ease of exposition, we report the findings for peripersonal and extrapersonal space separately, even though data for each viewing distance were obtained during a single testing session. We first report the direct effects of prismatic adaptation, and compare open-loop pointing responses obtained in the pre- and post-adaptation phases. We then report the effects of prismatic adaptation on spatial judgements of horizontal extent, as measured by the landmark task. We focus our discussion exclusively on the accuracy of responses yielded by this test, as the response time data revealed no significant effects of interest. In addition, because preliminary analyses of variance failed to reveal any significant effect of the hand used during adaptation, or of the horizontal position of line stimuli in the landmark task, these factors are not considered further here.

3.1. Development of prismatic adaptation (direct effects)
Displacement errors made during prismatic exposure were pooled for pointing responses made to left and right targets. Participants rapidly improved their pointing accuracy following an initial bias in the direction of prismatic displacement. They reached an asymptote after approximately 15 trials, which was maintained for the remainder of the adaptation period.
These results demonstrate that participants in both the left- and right-prism conditions were able to reduce their pointing errors over trials, thus compensating for the lateral displacement of the visual field induced by the prisms.

3.2. Influence of prismatic adaptation on straight-ahead pointing (aftereffects)

Adaptive aftereffects on straight-ahead pointing were analysed in order to verify that participants had adapted to the optical displacement. Their pointing accuracy under open-loop conditions (i.e. without visual feedback) was compared for pre-adaptation and post-adaptation conditions. Fig. 2 shows the change observed in the spatial location of straight-ahead pointing for each individual, separately for left- and right-prismatic displacements. For the left-shift condition (Fig. 2A), 14 of the 16 participants showed the expected rightward aftereffect, whereas two participants showed anomalous leftward deviations. Overall, for the left-prism group perception of straight ahead shifted significantly to the right from pre-adaptation ($M = 0.43$ mm [0.04˚], S.D. = 36.23) to post-adaptation ($M = 38.77$ mm [3.74˚], S.D. = 41.08), $F(15) = 14.61, P < 0.05$.

For the right-shift condition (Fig. 2B), 15 participants showed the expected leftward aftereffect; only one participant showed an anomalous rightward aftereffect. Overall, for the right-prism group perception of straight ahead shifted significantly to the left between pre-adaptation ($M = 22.03$ mm [2.13˚], S.D. = 44.25) and post-adaptation testing ($M = -13.15$ mm [-1.27˚], S.D. = 38.53), $F(1, 15) = 28.37, P < 0.001$.

3.3. Influence of prismatic adaptation on the landmark task

Data obtained from the landmark task were analysed separately for the left- and right-prism groups. One-way repeated measures ANOVAs were performed on data from peripersonal and extrapersonal space conditions, comparing subjective midpoint judgements in pre- and post-adaptation phases. The subjective midpoint was determined as the transection offset at which the frequency of ‘left’ responses was equal to 50%, as determined by a sigmoid function fitted individually to each participant’s data (see Fig. 3).

3.4. Peripersonal space

Fig. 4 shows performance on the landmark task plotted for each participant in the left-prism group, with separate fitted-sigmoid curves for pre- and post-adaptation phases.

There was a significant rightward shift of the subjective mid-
Fig. 4. Performance on the landmark task for the left-prism group (peripersonal space). Separate panels show individual data for each of the 16 participants (numbered). Curves are best-fitting sigmoid functions relating the proportion of left responses to the transection offset in pre-adaptation (filled symbols) and post-adaptation (open symbols) conditions. Vertical bars represent ±1 S.E.

This rightward shift was apparent in 10 of the 16 participants.

Fig. 5 shows individual performances on the landmark task for the right-prism group. Exploratory analysis of individual results revealed that the sigmoid function yielded a poor fit to the data of Participant 6 (see Fig. 5), whose accuracy was more than three standard deviations from the group mean in both pre- and post-adaptation phases. The data from Participant 6 were therefore excluded from further analysis. For the remaining 15 participants, there was no significant shift in the subjective midpoint following adaptation, $F(1, 14) = 0.98, n.s.$

A correlation analysis was performed to examine whether participants with larger biases in straight ahead judgements (open-loop pointing) also showed larger perceptual aftereffects on the landmark task. For participants adapted to left-prisms, there was no significant correlation between the magnitude of proprioceptive aftereffects in straight ahead judgements and the size of the visual aftereffect in the landmark task, $r = 0.01, P = 0.98$. Similarly, there was no significant correlation between these two measures for participants adapted to right-prisms, $r = -0.03, P = 0.92$.

3.5. Extrapersonal space

Fig. 6 shows results for the landmark task performed in extrapersonal space, plotted individually for each participant in the left-prism group, with separate fitted curves representing pre- and post-adaptation phases. As for the findings in peripersonal space, there was a significant rightward shift in subjective midpoint judgements in extrapersonal space following adaptation, $F(1, 15) = 4.89, P < 0.05$, which was equivalent to 0.74′ of visual angle or 0.19 mm. This rightward shift was apparent in 11 of the 16 participants.

Fig. 7 shows individual performances on the landmark task in extrapersonal space for the right-prism group. Exploratory analysis of individual results revealed that the sigmoid function again yielded a poor fit to the data from Participant 6 (see Fig. 7), whose data were therefore excluded from further analysis. In contrast to the null effects of right-prism adaptation on landmark judgements in peripersonal space, there was a significant and unexpected rightward shift of the subjective midline in extrapersonal space, $F(1, 14) = 16.33, P < 0.001$, which was equivalent to 1.54′ of visual angle or 0.58 mm. Note that the rightward shift in landmark judgements following right-prism adaptation, which was apparent in 12 of the 16 participants,
Fig. 5. Performance on the landmark task for the right-prism group (peripersonal space). Separate panels show individual data for each of the 16 participants (numbered). See Fig. 4 for further details.

is opposite to that observed in the straight-ahead pointing task, for which there was a significant leftward deviation after adaptation (see Fig. 2B). We speculate on the possible reason for this dissociation in Section 4.

As was the case for peripersonal space, there was no significant correlation between the magnitude of proprioceptive aftereffects in straight ahead judgements and the size of the visual aftereffects in the landmark task for participants adapted to left-prisms, $r = 0.24$, $P = 0.37$ or right-prisms, $r = 0.01$, $P = 0.98$.

4. Discussion

The purpose of this study was to examine whether visuomotor adaptation to a lateral shift of the visual field can influence visual judgements of spatial extent in normals. Our findings confirm those of Colent et al. [2] by showing that bisection judgements on the landmark task are shifted significantly to the right following adaptation to left-deviating prisms. Our results are also consistent with Colent et al.'s finding that adaptation to a right-prismatic shift does not induce a corresponding bias in normals, at least in peripersonal space, implying some asymmetry in the aftereffects induced depending on the direction of the lateral distortion (cf. [2,31]). In our study, the horizontal locations of landmark stimuli were altered from trial to trial to ensure that participants could not use their body midline directly to judge whether a transection mark was displaced to the left or right of a line’s midpoint. In addition, we projected all stimuli onto a uniform surface in an otherwise darkened room to minimise possible contamination by extraneous cues in the surrounding environment.

Crucially, our study shows for the first time that perceptual aftereffects revealed by the landmark task extend to stimuli presented in extrapersonal space, i.e. beyond the immediate region within which visuomotor adaptation takes place. Following adaptation to left-deviating prisms, participants showed a right shift in their bisection judgements for lines presented in extrapersonal space, consistent with their post-adaptation bias in peripersonal space. This result suggests that although peripersonal and extrapersonal space may nevertheless alter representations of more distant extrapersonal space as well. This finding is consistent with a recent single-unit study of bimodal neurons in the macaque inferior parietal sulcus [13], which showed that visual receptive fields surrounding the monkey’s hand extended out into extrapersonal space when the animal used a hand-held tool to retrieve a food pellet beyond arms’ reach. Similar effects have been observed in patients with
spatial extinction following unilateral lesions. For instance, Maravita et al. [17] found that tactile extinction on the contralesional hand could be induced by a concurrent visual event on the ipsilesional side, provided the visual stimulus appeared in peripersonal space (see also [21]). Extinction was absent when the same ipsilesional visual event appeared beyond arm’s reach (i.e. in extrapersonal space), but was reinstated when the patient used a rod held in the ipsilesional hand to point to the visual target in extrapersonal space. Taken together, the results of these studies suggest that neural representations of peripersonal and extrapersonal space can be modified dynamically, either by altering intrinsic visuomotor correspondences, as in prism adaptation, or by extending peripersonal space extrinsically through tool use.

A surprising result to emerge from the present study was that following adaptation to right-deviating prisms, participants showed a significant right shift in their judgements on landmark stimuli presented in extrapersonal space. This paradoxical result, which was evident in 12 of the 16 participants, emerged despite the same individuals showing a left (i.e. opposite) deviation in their egocentric straight-ahead judgements. Our explanation for this effect is necessarily post hoc, as we had not anticipated such a dissociation prior to the study. Nevertheless, we believe the effect may be explained in terms of the different reference frames used for the landmark and open-loop pointing tests, and the differential impact of prismatic adaptation on these reference frames.

We propose that pointing errors arising from lateral shifts of the visual field during prism exposure are processed asymmetrically by the two hemispheres, in a manner analogous to that claimed for shifts of spatial attention. Studies of attention suggest that the right hemisphere controls spatial orienting in both the left and right hemispaces, whereas the left hemisphere controls orienting only in the right (contralesional) hemispace [3,11,38]. Similarly, we suggest that during prismatic adaptation the right hemisphere is sensitive exclusively to errors on the right of the target. The effect of this error signal, which is critical for recalibrating spatial correspondences between vision and proprioception, is to update the current representation of space by suppressing visuomotor processes in the hemisphere responsible for signalling the error.

In this study, we used horizontal line bisection to measure the effects of spatial remapping due to prismatic adaptation. The landmark task, which emphasises allocentric coding by virtue of the varying horizontal location of the lines, has been shown preferentially to activate the right hemisphere.
A clear, if initially counterintuitive, prediction based on this account is that adaptation to either left- or right-prisms should suppress spatial representations in the right hemisphere more than the left, thus inducing a rightward shift in bisection judgements [6,15]. Note that this rightward shift is precisely what was found for both left- and right-prism conditions in extrapersonal space, and for the left-prism condition in peripersonal space. Viewed from this perspective, the only anomalous result to emerge from the present study, and that of Colent et al. [2], is the absence of a significant rightward shift for landmark stimuli presented in peripersonal space, following adaptation to right-deviating prisms.

We suggest that the otherwise ubiquitous rightward bias in allocentric encoding, as revealed by the landmark task, is attenuated by an opposing egocentric bias which dominates processing within peripersonal (reaching) space. Recall that the effects of prismatic adaptation on egocentric coordinates, as measured by participants’ open-loop judgements of straight ahead, were always biased in a direction opposite to that of the prismatic deviation, and with a magnitude that was symmetrical for left and right deviations (cf. Fig. 2A and B). Moreover, for both left- and right-prism groups, there was no significant correlation between estimates of straight ahead pointing and visual bias on the landmark test, in either peripersonal or extrapersonal space. Since representations of peripersonal space are likely to rely more on egocentric than allocentric coordinates [25], it follows that after exposure to right-prisms a leftward bias in egocentric coding will oppose the predicted rightward bias on the landmark task, and attenuate any effect of adaptation. This egocentric contribution should be significantly reduced when the landmark stimuli are presented in extrapersonal space, and so the rightward bias is revealed. Fig. 8 illustrates our explanation for the effects of right- and left-prismatic adaptation in peripersonal and extrapersonal space. Note that the opposition between the direction of allocentric and egocentric biases induced by right-prisms only arises in peripersonal space, consistent with our findings.

Though necessarily speculative at this stage, our account for the effects of prism adaptation on visuospatial perception generates testable predictions. For instance, if we are correct that the right hemisphere processes both left and right spatial errors during adaptation, whereas the left processes errors to the right only, then right hemisphere damage should attenuate aftereffects to left-deviating prisms. This prediction is supported by the work of Rossetti and co-workers [31,34], who have shown repeatedly that left-prismatic adaptation does not affect visual perception in right hemisphere patients with spatial neglect. As a corollary of this prediction, adaptation effects in left hemisphere cases should be relatively symmetrical for left- and right-deviating prisms,
on tasks such as chimeric faces and grey scales [18–20,23], adaptation to optical wedge prisms would be useful to test the effects of prism adaptation observed here for different measures of visual space perception. This rightward bias is attenuated when stimuli are presented in peripersonal space, however, due to an opposing egocentric bias (open arrows) toward the left induced by right-prism adaptation.

since the intact right hemisphere is able to process error signals arising on either side of the target. To our knowledge no studies have compared the effects of left- versus right-prismatic adaptation on perception in left hemisphere patients (though see [37]). The same predictions concerning hemispheric asymmetries could readily be tested using focal transcranial magnetic stimulation (TMS) over appropriate left and right hemisphere (parietal?) sites. It would also be of interest to examine whether judgements of straight ahead, as revealed by open-loop pointing, differ in peripersonal and extrapersonal space. This could be done by having participants indicate their perception of straight ahead by pointing (as in the present study), and by using a stick that extends the effective reaching distance into extrapersonal space (see [13,17]).

It will also be important in future studies to examine the possible effect of prism adaptation on the oculomotor system, and in particular whether the perceptual effects observed here for different measures of visual space perception, it would be useful to test the effects of prism adaptation on tasks such as chimeric faces and grey scales [18–20,23], which have revealed consistent perceptual biases in normals due to underlying functional hemispheric asymmetries. The chimeric faces task requires participants to judge which of two vertically aligned faces appears to have a happier expression. Each face is a composite in which the left half is happy and the right half neutral, and vice versa for the other face in the pair [20]. Similarly, the grey scales task requires participants to judge which of two rectangles, shaded from black on the left to white on the right, and vice versa, is darker overall [19]. For both tasks, normals show a consistent leftward bias (i.e. they tend to select the item from a pair in which the critical feature appears on the left), perhaps reflecting right hemisphere mediation [18–20,23]. Patients with right hemisphere lesions show an anomalous rightward bias on the same tasks [18–20].

To summarise, we have shown that a short period of visuomotor adaptation to optical wedge-prisms induces a small but consistent bias in normal observers’ judgements of spatial extent, and that this bias extends into extrapersonal space, beyond the immediate spatial region within which the adaptation occurs. We speculate that the direction of spatial bias exhibited following adaptation is influenced by the reference frame used by observers to perform the spatial judgements. We suggest that an underlying hemispheric asymmetry in the processing of spatial error signals arising during prismatic adaptation may explain the pattern of aftereffects observed in normal observers, and in unilateral lesion patients.

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