Position matching between the visual fields in strabismus

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The misalignment of visual input in strabismus disrupts positional judgments. We measured positional accuracy in the extrafoveal visual field (1°–7° eccentricity) of a large group of strabismic subjects and a normal control group to identify positional distortions associated with the direction of strabismus. Subjects performed a free localization task in which targets were matched in opposite hemifields whilst fixating on a central cross. The constant horizontal error of each response was taken as a measure of accuracy, in addition to radial and angular error. In monocular conditions, all stimuli were viewed by one eye; thus, the error reflected spatial bias. In dichoptic conditions, the targets were seen by separate eyes; thus, the error reflected the perceived stimulus shift produced by ocular misalignment in addition to spatial bias. In both viewing conditions, both groups showed reliable over- and underestimations of visual field position, here termed a compression of response coordinates. The normal group showed compression in the left periphery, regardless of eye of stimulation. The strabismic group showed a visual field-specific compression that was clearly associated with direction of strabismus. The variation in perceived shift of strabismic subjects was largely accounted for by the biases present in monocular viewing, suggesting that binocular correspondence was uniform in the tested region. The asymmetric strabismic compression could not be reproduced in normal subjects through prism viewing, and its presence across viewing conditions suggests a hemifield-specific change in spatial coding induced by long-standing ocular misalignment.

Introduction

When the eyes are misaligned, an object at the center of gaze is imaged on a peripheral location on the deviating retina, producing double vision (diplopia). The fixing eye perceives the object as straight ahead, but the deviating eye perceives it as shifted from center in a direction given by the ocular misalignment. Strabismic individuals rarely experience diplopia because the aberrant percept is suppressed (interocular suppression: Bagolini, 1974; Economides, Adams, & Horton, 2012; Jampolsky, 1955; von Noorden & Campos, 2002), and because in certain cases the spatial coordinates of the two eyes are realigned in an adaptation known as anomalous retinal correspondence. The perceptual consequences of ocular misalignment are, however, evident in spatial judgments measured under monocular viewing conditions, and in dichoptic viewing where input to the eyes is dissociated. Performance in such conditions reveals disruptions of positional encoding both in the absence of competing input from the fellow eye (e.g., Bedell & Flom, 1981, 1983), and when input from the two eyes must be combined (Fronius & Sireteanu, 1989; Lagrèze & Sireteanu, 1991). Here, we characterize these disruptions in both viewing conditions, to identify a systematic pattern associated with the angle of strabismus.

Positional disruptions in monocular viewing have been shown in directionalization and partitioning tasks measuring the locus of subjective alignment, or bisection between two spatial references (Bedell & Flom, 1981,

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1983; Bedell, Flom, & Barbeito, 1985; Demanins & Hess, 1996; Fronius & Sireteanu, 1989; Levi & Klein, 1983). Strabismic observers show large constant directionalization errors, over- and underestimations of spatial extent, and a high degree of imprecision in both sides of the visual field. The larger-than-normal error found in these tasks is thought to reflect warping, compression, and expansion of two-dimensional space and patterns seen by the deviating eye (Bedell & Flom, 1981, 1983; Bedell et al., 1985; Sireteanu, Lagreze, & Constantinescu, 1993), and has been proposed to underlie the salient losses in visual acuity that occur in strabismic amblyopia (Bedell & Flom, 1981, 1983). In monocular viewing, all spatial references are seen by one eye. Therefore, the constant error reflects spatial biases that differ from the perceived shifts produced by binocular misalignment per se.

When similar tasks are performed in dichoptic conditions, i.e., with the references seen separately by the two eyes, the constant error now includes the perceived shift of the stimulus produced by the binocular misalignment, in addition to the spatial biases measured in monocular conditions. This shift is measured directly in clinical tests of retinal correspondence by having subjects superimpose foveally presented dichoptic targets. In strabismic subjects with normal retinal correspondence, the targets appear superimposed when they are offset by an amount equal to the angle of misalignment. When the offset is less than the strabismus angle, retinal correspondence is termed anomalous. Thus, the constant error in dichoptic interval and alignment judgments is associated with the amount of binocular correspondence at the tested locations. These methods, and horopter measurements, have suggested variations across the visual field in retinal correspondence of strabismic individuals (Burian, 1941; Flom, 1980; Mansouri, Hansen, & Hess, 2009; Sireteanu & Fronius, 1989). Therefore, one of the goals of the present work was to assess whether such variation could be detected in dichoptic positional judgments outside the foveal region.

The constant error of monocular and dichoptic positional judgments was measured here in a free localization task, in which a positional match was made between targets in opposite hemifields. Since the match was free to vary in both the radial and tangential directions, the task involved both a spatial interval and an alignment judgment in each response. In previous work, we have used this task to infer cortical mapping properties in amblyopia from the precision of positional judgments across the visual field (Hussain et al., 2015). We now focus on the accuracy of positional judgments to identify spatial biases that depend clearly on strabismus direction, suggesting predictable changes in the cortical spatial representation.

Materials and methods

Subjects

Thirty-two strabismic subjects and 20 subjects with normal visual alignment were tested. Tables 1 and 2 provide clinical details for the strabismic subjects: 10 left esotropes, 11 right esotropes, seven left exotropes, and two right exotropes. Normally aligned subjects were undergraduate students and research staff at the University of Nottingham. All subjects were informed of the purpose and procedure of the study. Strabismic subjects provided a detailed ophthalmic history and were examined by a registered optometrist prior to testing. Ocular movements and ocular alignment for distance and near were measured using the cover test, a reliable clinical method of determining the angle of deviation (Fogt, Baughman, & Good, 2000; Johns, Manny, Fern, & Hu, 2004). LogMAR acuity was measured using the ETDRS chart. Ocular deviation ranged from 2 to 20 prism diopters. Seven subjects had a deviation of 4 prism diopters or less (i.e., within the range of microstrabismus, see Table 1). None of the subjects had alternating strabismus. There was a significant positive correlation between the magnitudes of the angle of strabismus measured by the near and far cover test: $r(29) = 0.83$, $p < 0.0001$; $t = 7.92$; 95% CI = [0.67–0.91]. All subjects were amblyopic (0.20 LogMAR or more difference in acuity between the eyes). Best optical correction was determined by subjective refraction for all strabismic subjects. Thirteen of 32 strabismic subjects (indicated in Table 1) and seven of 20 normally aligned subjects provided monocular data for both eyes. Dichoptic data were excluded for two of 32 subjects who showed paradoxical diplopia (indicated in Table 1).

Apparatus and stimuli

The experiment was performed with an Apple G5 iMac computer, running PsychoPy (Peirce, 2007). The monitor was a Trinitron Dell P1130 with a screen width of 40 cm and resolution of 1280 × 1024 pixels. Mean background luminance was 41 cdm^{-2}. Viewing distance was 114 cm. The fixation mark was a black cross subtending 0.38° of visual angle, and the target and response stimuli were dots of uniform luminance subtending 0.28° of visual angle. To counteract interocular suppression, the dots flickered at 8 Hz. In *dichoptic viewing*, the display was viewed through monochromatic red-green filters that were matched to the spectral profile of the stimuli such that the target and response dots were viewed separately by each eye. Kodak Wratten filters (numbers 58 and 29) were used. The red filter (number 29) transmits only wavelengths above 600

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ID	Age, sex	Eye, alignment (prism diopters)	Patching, operation	Refractive error	LogMAR
CB**	57 m	LSOT 4	yes, no	OD +3.00/−0.25 × 75	−0.08
				OS +6.00DS	0.64
CG	70 m	LSOT 10	yes, yes	OD +5.25/−0.50 × 175	−0.08
				OS +8.00/−1.25 × 65	0.30
DR	33 f	LSOT 20	yes, no	OD +4.50DS	0.00
				OS +6.50/−0.50 × 180	0.60
HM	27 f	LSOT 6	yes, no	OD +4.50/−0.50 × 15	−0.14
				OS +3.00/−0.25 × 35	0.20
JA	21 f	LSOT 8	yes, yes	OD +3.50/−0.50 × 145	−0.02
				OS +4.50/−0.75 × 45	0.54
JC2	45 m	LSOT 14	yes, yes	OD +0.25/−1.00 × 175	0.00
				OS +0.75/−0.25 × 50	0.50
KA**	45 m	LSOT 18	yes, no	OD plano	−0.04
				OS plano/−0.75 × 40	0.62
KG**	21 f	LSOT 16	yes, yes	OD +5.25/−0.75 × 110	−0.06
				OS +6.25/−0.75 × 80	0.36
LG**	48 F	LSOT 18	no, no	OD +0.75/−0.50 × 15	0.02
				OS +1.75/−2.00 × 150	1.12
PB**	67 m	LSOT 6	yes, no	OD +6.75/−1.75 × 85	0.08
				OS +6.75/−1.75 × 80	0.38
BR	32 m	RSOT 6	yes, yes	OD +3.25/−2.00 × 165	0.34
				OS +3.75/−2.25 × 180	−0.04
BS*	32 m	RSOT 2	yes, no	OD −1.25/−1.00 × 120	0.68
				OS −1.75/−0.50 × 85	−0.06
CG**	25 m	RSOT 12	yes, no	OD +1.25/−0.75 × 165	0.72
				OS −3.25/−1.00 × 180	0.02
JH**	21 f	RSOT 2	yes, yes	OD +2.75/−0.50 × 140	0.62
				OS +1.75DS	−0.06
JP**	35 m	RSOT 2	yes, no	OD +2.50/−0.50 × 130	0.32
				OS plano	0.02
MB	22 m	RSOT 5	no, no	OD +6.50/−1.75 × 5	0.38
				OS +4.50/−1.50 × 5	0.08
SC	62 m	RSOT 15	yes, no	OD +10.00/−1.50 × 100	1.06
				OS +8.00/−0.75 × 180	0.00
SE	17 m	RSOT 12	yes, no	OD +4.50/−0.75 × 105	0.48
				OS +3.00/−0.75 × 95	−0.08
SM**	34 m	RSOT 8	yes, no	OD −0.50DS	1.02
				OS −0.50/−0.50 × 160	0.00
SS**	33 m	RSOT 2	yes, no	OD −0.75/−0.75 × 103	0.98
				OS −1.25DS	−0.10
ST	37 m	RSOT 16	yes, yes	OD +3.50/−1.50 × 170	0.56
				OS −3.25/−0.25 × 30	−0.06
CC*	43 m	LXOT 12	yes, no	OD +0.75/−0.50 × 180	−0.08
				OS +6.75/−2.75 × 12.5	1.00
CT	19 m	LXOT 10	yes, yes	OD +0.25/−0.25 × 150	0.02
				OS +7.75/−0.25 × 68	1.58
IB	45 m	LXOT 14	yes, no	OD +0.25/−0.25 × 110	−0.14
				OS +4.50DS	0.52
JC1	33 m	LXOT 3	yes, yes	OD +1.00/−0.25 × 70	0.04
				OS +8.50/−4.50 × 65	1.00
JN	20 m	LXOT 5	yes, no	OD plano	−0.02
				OS +5.00/−3.50 × 20	0.80

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ID	Age, sex	Eye, alignment (prism diopters)	Patching, operation	Refractive error	LogMAR
JO**	20 m	LXOT 12	yes, no	OD −2.50/−0.50 × 30	0.06
				OS plano/−3.50 × 160	1.04
KR**	21 m	LXOT 8	yes, no	OD plano	−0.14
				OS +3.50/−1.75 × 20	0.58
MP*	24 m	LXOT 16	yes, no	OD −1.50DS	−0.10
				OS +4.00/−1.50 × 180	1.00
RA*	22 f	LXOT 6	yes, yes	OD +0.50/−0.25 × 110	−0.06
				OS +0.25DS	0.42
GJ	29 m	RXOT 4	yes, yes	OD +4.75/−2.50 × 10	1.06
				OS +0.75/−0.25 × 10	−0.06
RB**	28 f	RXOT 6	no, no	OD +3.50/−5.50 × 10	0.34
				OS +0.50DS	−0.20

Table 1. Strabismic subject clinical details. *Notes*: LSOT = left esotropia; LXOT = left exotropia; RSOT = right esotropia; RXOT = right exotropia. *Excluded from analyses. **Dichoptic and monocular conditions.

nm, and green filter (number 58) transmission is between 470–610 nm. The background was calibrated to ensure no crosstalk between filters. In *monocular viewing*, both dots were set to pass through a single filter, and the entire display was viewed through one eye, with the fellow eye patched. Target locations were sampled from one of eight polar angles (22.5°, 67.5°, 112.5°, 157.5°, 202.5°, 247.5°, 292.5°, and 337.5°), and four eccentricities (1°, 3°, 5°, and 7° of visual angle), yielding 32 stimulus locations. Visual field position was calculated assuming a gaze-normal display (i.e., 1° = 2 cm at 114 cm viewing distance for both eyes). The stimulus locations are shown in Figure 1.

Procedure and tasks

All subjects were fitted with best optical correction using trial lenses. No contact lenses were used. Subjects were then seated in a darkened room in front of the display, with viewing stabilized by a chin-rest. Several practice trials were given before the session began.

Each trial comprised a fixation cross in the center of the screen, the target dot positioned randomly at one of the 32 locations, and the response dot positioned on the fixation cross. The subject used the mouse to move the response dot to a position reflected across the target in the opposite hemifield (i.e., across both vertical and horizontal meridians, diagonally), such that the fixation cross bisected the two points and the three stimuli fell in a straight line. Subjects were instructed to maintain fixation throughout the trial. Response time was unlimited and the response was registered by keypress. Hence, the task comprised a dual bisection and alignment judgment, with the final position of the images in the two eyes in opposite hemifields (see Figure 1).

In dichoptic conditions, the target was always green, and for the strabismic group, always viewed by the fixing eye; the response dot was always red and viewed by the deviating eye. Target and response dots were randomized between the eyes of normal subjects. Only the fixation cross was exposed to both eyes. We confirmed that subjects saw only one cross (i.e., the diplopic image of the cross was either suppressed, or in anomalous correspondence with the fixing eye under these viewing conditions). None of the subjects included here reported diplopia of the fixation cross in dichoptic viewing.

Predicted response shifts

Figure 1 shows the retinal comparisons underlying the matching judgment for a subject with normal ocular alignment (Figure 1B, left) and for a strabismic subject

	LSOT	RSOT	LXOT	RXOT	Rightward (LSOT, RXOT)	Leftward (RSOT, LXOT)
N	10	11	7	2	12	18
Number of males	5	10	7	1	6	17
Mean age (years)	43	32	29	29	41	31
Mean alignment (PD), NCT	12	8	9	5	11	8
Mean alignment (PD), DCT	9	7	9	5	9	8
Mean visual acuity (LogMAR), strabismic eye	0.52	0.65	0.70	0.91	0.55	0.75

Table 2. Strabismic subject summary. *Notes*: PD = prism diopter; NCT = near cover test; DCT = distance cover test.

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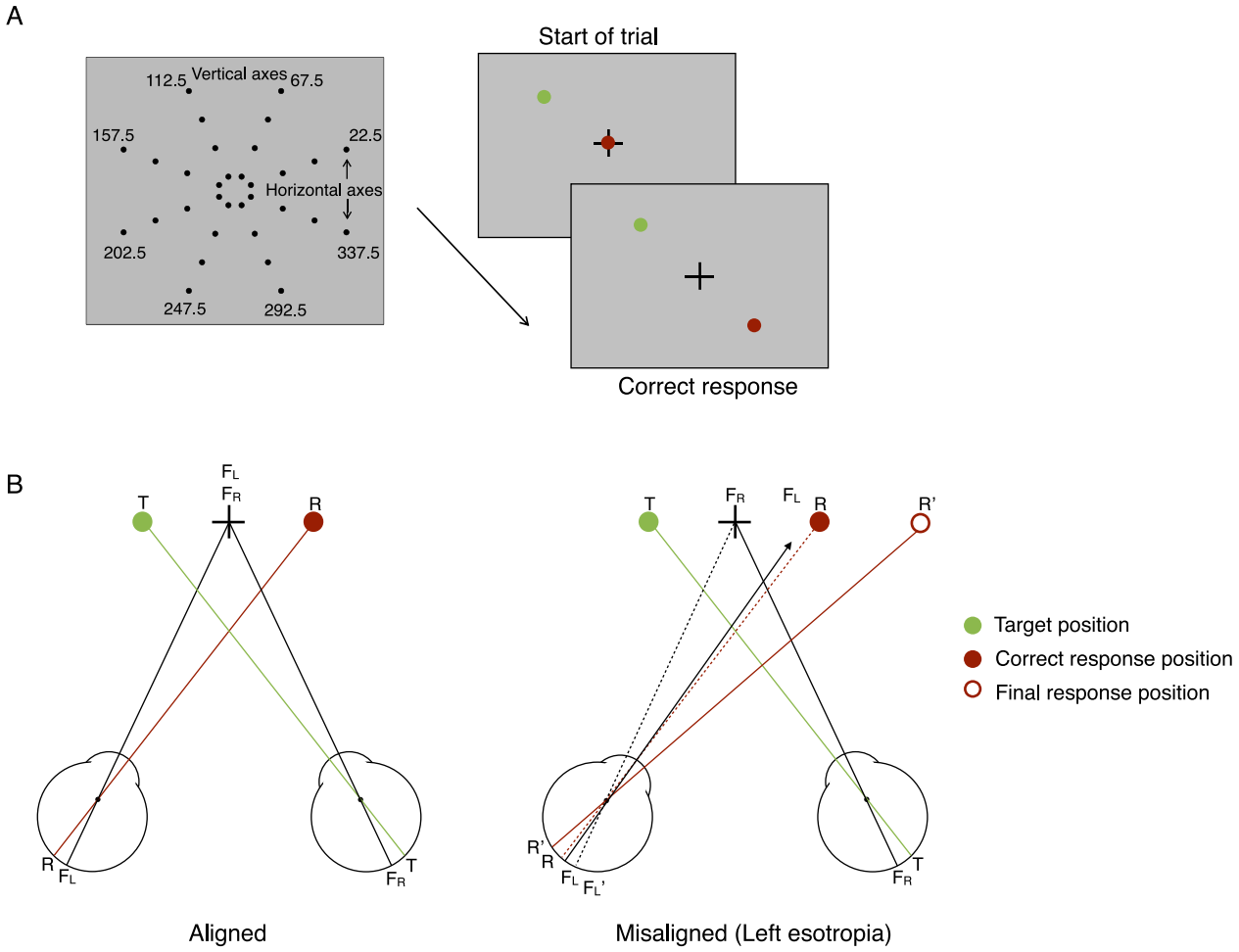


Figure 1. (A) Stimulus positions and schematic of tasks. Thirty-two locations were tested (4 eccentricities × 8 polar angles, shown in degrees). Target axis (vertical vs. horizontal) was defined by proximity to the vertical or horizontal meridian. The task was to position the response dot diagonally opposite the target dot, whilst maintaining fixation. The response dot could be moved along both radial and polar angle directions; hence, each trial combined a bisection and an alignment judgment. (B) Schematic retinal geometry of dichoptic viewing for a subject with normal ocular alignment (left), and for a subject with left esotropia. The normal subject performed the task by equating the distance F_R-T and F_L-R, placing the response dot at R. For an esotropic subject with normal retinal correspondence (F_R and F_L correspond), the response is displaced from R to R'. For an esotropic subject with harmonious anomalous retinal correspondence (F_R and $F_L{}'$ correspond), the response is not displaced from R. For an esotropic subject with unharmonious anomalous retinal correspondence, the response is displaced to a location between R and R'; see text for further detail. In monocular viewing, all stimuli projected to one eye, and the subject equated nasal and temporal distances to the foveal fixation cross. No displacement is predicted.

with esotropia of the left eye (i.e., a nasalward deviation of the left eye; Figure 1B, right). We assume that a normal subject performed the task by equating the distances F_R-T and F_L-R on each retina, for any given target position (T), response position (R), and with F_R and F_L representing the fovea (or fixation) in each eye.

Normal retinal correspondence (NRC)

In a strabismic subject with normal retinal correspondence and left esotropia (Figure 1B, right), the anatomical foveas F_L and F_R correspond. Hence, the final position of the response is given by the perceived equivalence between distances F_R-T and F_L-R' (and not F_L-R) on the retina. Since the response dot R is imaged nasally on the retina toward F_L due to the inward deviation of the eye, it is perceived temporally (leftward) in visual space relative to its true position. Hence, the subject moves the response dot rightward on the screen (temporalward on the retina) to null the perceived leftward offset. Following the same principle, responses are displaced leftward in the case of right eye esotropia with NRC. In exotropia, the relationship is because the eye deviates outward (temporally). Hence, the response dot is imaged temporally away from the anatomical fovea on the deviating retina, and

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perceived as shifted nasally away from its true position. This produces a temporal displacement of responses (i.e., rightward for right eye exotropia, and leftward for left eye exotropia). In general, in NRC, when the eyes are dissociated, the perceived shift of the diplopic image (i.e., the subjective angle of deviation) equals the objective angle of deviation, and the angle of anomaly (i.e., the difference) is zero.

Harmonious anomalous retinal correspondence (HARC)

In a strabismic subject with HARC, F_L' and F_R correspond and responses would be based on the perceived equivalence between F_L'-R and F_R-T. In a subject with no additional spatial distortions, there would be no shift of responses from the correct response position. In HARC, the subjective angle is zero, and the angle of anomaly equals the objective angle of deviation.

Unharmonious anomalous retinal correspondence (UHARC)

In subjects with UHARC, an intermediate point between F_L and F_L' corresponds to F_T. Therefore, the response is placed between R and R'. Here, the angle of anomaly is greater than zero but less than the objective angle.

Results

Individual positional maps

Figure 2 shows maps of positional accuracy of individual normal and strabismic subjects. The mean response at each location was computed by averaging the x and y coordinates of the seven trials at each location. Normal subjects were accurate and precise in both viewing conditions, with a slight decline in performance in the periphery. The variability of responses is shown by the individual data points shown as gray crosses. Strabismic subject maps were noisier, particularly for the deviating eye (Figure 2 left eye columns for left esotropes, and right eye columns for right esotropes), and in dichoptic viewing (rightmost column for all subjects). Dichoptic maps were shifted in the direction consistent with ocular deviation for most subjects, except instances where negligible shift was present despite the ocular misalignment (e.g., subjects KR and RB), suggesting harmonious anomalous retinal correspondence in these subjects. For all subjects, the magnitude of the average dichoptic shift across locations was less than that predicted by the objective angle of deviation. Furthermore, the average shift across subjects was less than one-sixth of the average objective angle (see Results). A part of this discrepancy may have arisen from the variation in objective angle that can occur over time and across viewing conditions, which was not measured here. Alternatively, the discrepancy suggests a realignment of binocular spatial coordinates in these subjects, in addition to potential variations in objective angle.

Error calculation

X error, radial error, and angular error were calculated for every subject. Radial and angular error are shown alongside x error in the Figures 3, 4, and 6 to illustrate the broad range of spatial biases affecting performance on this task.

The x coordinate of each positional judgment is related to polar position as

$$x = r\cos\theta \quad (1)$$

where r is the radius (or eccentricity) of the given position, and θ the polar angle in radians.

X error was defined as

$$x_{\text{error}} = x_{\text{response}} - x_{\text{correct}} \quad (2)$$

Radial error was defined as

$$r_{\text{error}} = r_{\text{response}} - r_{\text{correct}} \quad (3)$$

Angular error was defined as

$$\theta_{\text{error}} = \theta_{\text{response}} - \theta_{\text{correct}} \quad (4)$$

All measures of error were signed and expressed in degrees of visual angle (x_{error}, r_{error}, θ_{error}), calculated from the errors in pixel units ($\tilde{x}_{\text{error}}$, $\tilde{r}_{\text{error}}$, $\tilde{\theta}_{\text{error}}$). At a screen resolution of 1280×1024 pixels and viewing distance of 114 cms, 1° of visual angle corresponded to 64 pixels (i.e., 1.067 arc minutes/pixel) therefore x_{err} and r_{err} in degrees of visual angle are given by $\tilde{x}_{\text{error}}/64$, $\tilde{r}_{\text{error}}/64$, and θ_{err} in degrees of visual angle is given by $r\tilde{\theta}_{\text{error}}/64$.

Data analysis

The 32 tested locations (4 eccentricities × 8 polar angles) were reduced to 16 locations (4 eccentricities × 2 visual fields × 2 axes) for every subject, by averaging the upper and lower visual field locations separately for the horizontal and vertical axes in each visual field (left or right). Near-horizontal axes (henceforth horizontal axes), include the four polar angles near the horizontal meridian, two for the right visual field (22.5°, 337.5°), and two for the left visual field (157.5°, 202.5°). Near-vertical axes (henceforth vertical axes), include the four

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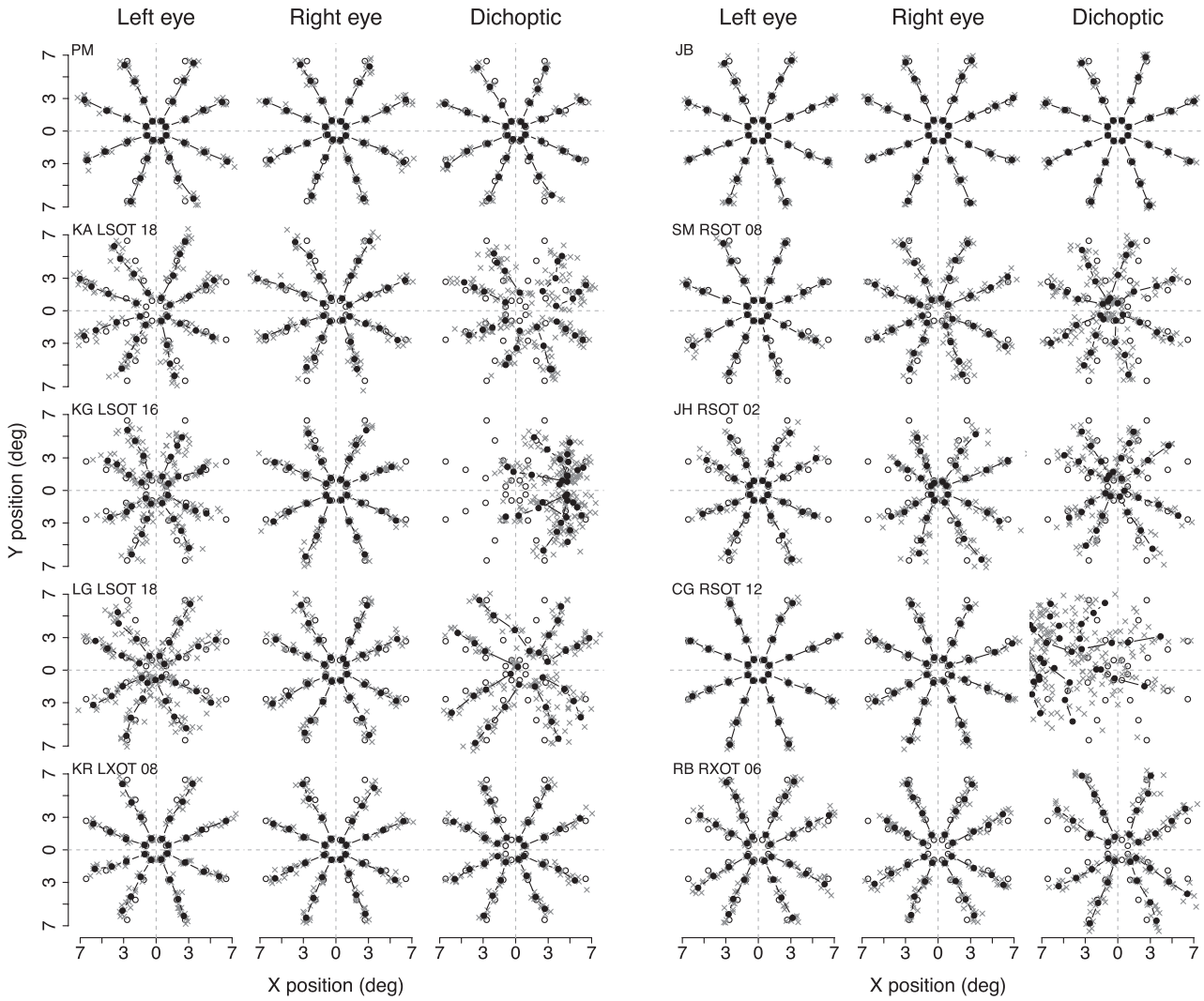


Figure 2. Monocular and dichoptic positional maps of normally aligned and strabismic subjects. Top row: Normally aligned subjects. Rows 2–5: Strabismic subjects. Left panels: Strabismic subjects with left eye deviation (rows 2–4, esotropia; row 5, exotropia). Right panels: strabismic subjects with right eye deviation. Subject initials and strabismus angle in prism diopters shown at top left. Strabismus angle was measured using the near cover test. White symbols: tested location. Black symbols: average response at tested location. Gray crosses = individual trials; LSOT = left esotropia; RSOT = right esotropia; LXOT = left exotropia; RXOT = right exotropia.

polar angles near the vertical meridian, two for the right visual field (112.5°, 247.5°), and two for the left visual field (67.5°, 292.5°; see Figure 1).

X error (alternately *x* shift) and radial error are shown as a function of target eccentricity, visual field (left, right), and axes (horizontal, vertical). Angular error is shown against polar angle, separately for the four eccentricities. The differences in *x* error were evaluated with mixed repeated-measures analyses of variance (ANOVA), with Eccentricity (1°, 3°, 5°, 7°), Axis (horizontal vs. vertical), and Visual Field (left vs. right; or leading vs. trailing; see further in article) as within subjects factors. Eye (left vs. right; strabismic vs. fellow) was also treated as a within-subjects factor. Group (normal vs. strabismic), Strabismus Direction (left vs. right), and Strabismus Type (esotropia vs. exotropia) were between subjects factors. Significant interaction effects were decomposed with simple main effects and *t* tests evaluated at an alpha level of 0.05.

The normal monocular and dichoptic patterns are described first, followed by strabismic monocular performance for each eye, and finally, strabismic dichoptic performance.

Normal monocular and dichoptic performance

Figure 3A shows the mean monocular and dichoptic positional maps of the normal group. Seven subjects performed the task monocularly (right and left eye, both), and a separate group of 20 subjects performed the task dichoptically. Two subjects performed the task in all conditions (shown in Figure 2). Normal

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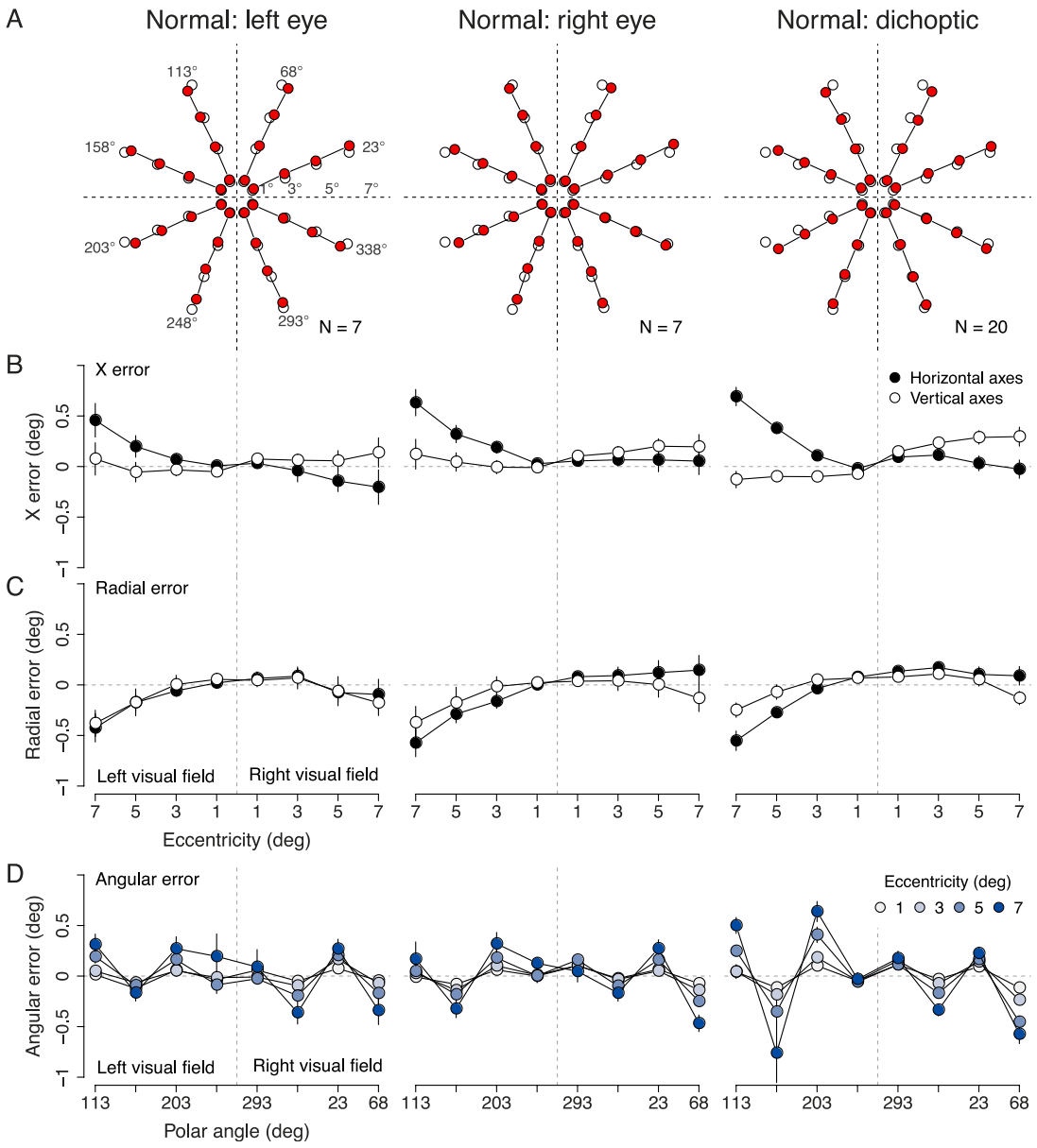


Figure 3. (A) Mean positional maps of the normally aligned group: monocular left eye (left panels), monocular right eye (middle panels), and dichoptic viewing (right). White symbols: correct response location. Red symbols: average response position of the group. (B) Mean signed *x* shift plotted against eccentricity, separately for the left and right visual field, and separately for the horizontal and vertical axes (solid symbols: horizontal axes, open symbols: vertical axes). Positive shifts indicate rightward shifts; negative shifts indicate leftward shifts. (C) Mean signed radial error plotted against eccentricity, same convention as (B). Positive error indicates expansion of responses; negative error indicates compression toward center. (D) Mean signed angular error plotted against polar angle, separately for the four eccentricities. All plots: Vertical dashed line divides the left and right visual field. Horizontal dashed line indicates zero error. Error bars show the standard error of the mean, smaller than symbol where not shown.

performance in both viewing conditions was accurate and precise, with accuracy within a tenth of a degree of visual angle on average across all points. However, accuracy varied systematically with visual field position. Figure 3B through D shows *x* error, radial error, and angular error in the left and right visual field. These figures confirm the presence of clear location-specific biases on all measures. Our focus was on *x* error. Positive *x* error at all points represents a rightward translation of responses, and negative error a leftward translation. Positive error at all points in the left visual field combined with negative error in the right visual field represents a contraction of responses toward the center, and the reverse indicates an expansion of responses. The contraction might also occur separately within each visual field, manifesting as an eccentricity-dependent pattern of peripheral contraction combined with central expansion, or the reverse.

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Figure 3B shows that in the monocular conditions x error was positive (rightward) on the horizontal axes in the peripheral left visual field, and less pronounced at other positions. This pattern was confirmed by a significant Eccentricity × Visual Field × Axis interaction, $F(3, 150) = 9.24$, $p < 0.0001$, in an analysis that included both eyes for each subject. The error overall appeared larger in the right eye than the left eye, but this difference did not achieve significance: Main effect of Eye, $F(1, 6) = 3.67$, $p = 0.10$. Eye did not interact significantly with the other variables ($p > 0.05$ for all interactions). Therefore, the monocular data were averaged over the left and right eyes. Further analyses showed that x error varied with visual field position only on the horizontal axes, confirmed by a significant Eccentricity × Visual Field interaction on the horizontal axes, $F(3, 18) = 7.70$, $p = 0.001$, but not the vertical axes, $F(3, 18) = 0.19$, $p = 0.91$. On the horizontal axes, there was a significant effect of Eccentricity in the left visual field, $F(3, 18) = 10.64$, $p = 0.0003$, but not the right visual field, $F(3, 18) = 0.95$, $p = 0.44$, confirming that this variation was confined to the left visual field. Tests of pairwise differences showed that in the left visual field, mean error at 7° eccentricity (0.54°) differed significantly from error at all other eccentricities (mean error at 1°, 3°, 5°: 0.01°, 0.13°, 0.25°); the other pairwise differences were not significant. Positively signed error indicates a contraction (alternately compression), of responses in the left horizontal visual field of both eyes of normal subjects.

A similar pattern was observed with the dichoptic data, with larger-than-average positive x error in the left periphery. The Eccentricity × Axis × Visual Field interaction was significant, $F(3, 190) = 31.87$, $p < 0.0001$, as was the Eccentricity × Visual Field interaction on the horizontal axes, $F(3, 57) = 32.68$, $p < 0.0001$, and in this case, the vertical axes, $F(3, 57) = 4.45$, $p = 0.007$. On the horizontal axes, there was a significant effect of eccentricity in the left visual field, $F(3, 57) = 45.05$, $p < 0.00001$, but not the right visual field, $F(3, 57) = 3.32$, $p = 0.09$. All pairwise eccentricity differences in error were significant in the left visual field (1°, 3°, 5°, 7° mean error: −0.01°, 0.11°, 0.38°, 0.69°). On the vertical axes, the effect of eccentricity was not significant in the left visual field, $F(3, 57) = 0.734$, $p = 0.54$, but it was significant in the right visual field, $F(3, 57) = 5.54$, $p = 0.002$. Mean error at 1° differed from all other eccentricities; none of the other pairwise differences were significant (1°, 3°, 5°, 7° mean error: 0.15°, 0.23°, 0.29°, 0.30°). These results suggest an expansion of responses on the vertical axes in the right visual field, in addition to compression of responses on the horizontal axes in the left visual field.

Figure 3C shows radial error at each position, using the same convention as in Figure 3B. There was a negative radial bias in the left visual field indicating radial compression on both the horizontal and vertical axes, consistent with the x error shown in Figure 3B. The radial compression on the vertical axes was accounted for by variation in y error, not shown. (Y error varied on the vertical axes between the upper and lower visual fields, unlike the left-right variation of x error). Figure 3D shows angular error across polar angle for the four eccentricities. The sign of the angular error alternated between positive and negative across polar angles, in a direction consistent with repulsion from the cardinal orientations and attraction toward the diagonals (see also Figure 3A). Hence, the variation in the response x position was affected by, and reflected in, radial and angular biases that depended strongly on visual field position.

Overall, normal x error followed a pattern of undershooting in the left horizontal visual field, consistent with a compression of responses in this region, both in monocular and dichoptic viewing. Radial error also showed left compression, but this compression was not confined to the horizontal axes.

Strabismic group: Monocular performance of strabismic and fellow eye

Figure 4A shows the monocular positional maps of subjects with left esotropia and right esotropia (five subjects each), separately for the deviating eye (Figure 4, left panels) and fellow eye (Figure 4, right panels). One right exotrope, and two left exotropes were also tested monocularly (data not shown). The plotting convention is the same as in Figure 3, but note the increase in scale for Figures 4B through D. Figure 4 suggests that the strabismic group showed similar biases as the normal group, with x compression on the horizontal axes, radial compression on both axes, and angular error that varied systematically with polar angle. Unlike the normal group, the compression for both strabismic groups was present in both visual fields, for both eyes. The strabismic and fellow eye of the two groups showed the same broad patterns on all three measures, but differed in certain locations. We first compare each eye of the strabismic group against a normal control group (separately for the left and right esotropes), and then evaluate the difference between eyes for the two groups. The phrase larger-than-normal where used refers to error magnitude.

To establish whether the strabismic pattern differed from normal, each eye of each strabismic group was compared against the respective normal group (e.g., RSOT deviating right eye vs. normal right eye, RSOT fellow left eye vs. normal left eye). A significant Eccentricity × Axis × Visual Field interaction suggests that the error varied along the three spatial dimensions as it did for the normal group. Higher order interactions of Group (strabismic vs. normal), Strabismus Direction (left vs. right), or Eye (strabismic vs. fellow) with Eccentricity,

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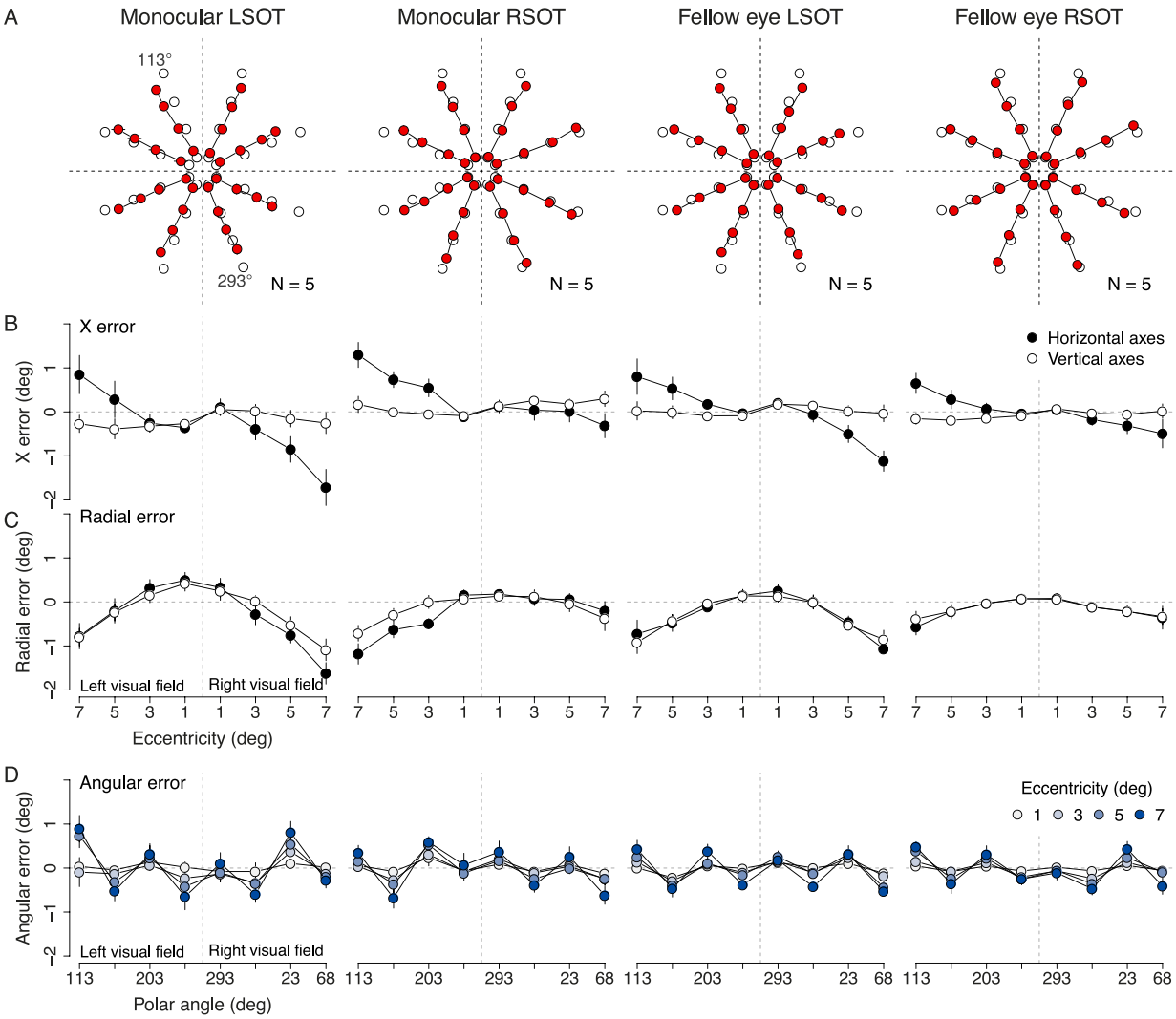


Figure 4. (A) Monocular positional maps of the strabismic group. Average performance of five left esotropes and five right esotropes shown separately for the deviating eye (left panels) and fellow eye (right panels) of each group. White symbols: correct position. Red symbols: Average response position. (B–D) *X* error, radial error and angular error for the above conditions, plotting conventions same as in Figure 3. Error bars show the standard error of the mean, smaller than symbol where not shown.

Axis, and Visual Field indicate that the pattern varied between groups or eyes. All significant interactions were decomposed with simple main effects and *t* tests, evaluated at an alpha level of 0.05. Due to the large number of follow up tests, only the highest order interaction statistic and the final summary result are reported. These comparisons are visualized in Figure 5A, which shows each group alongside normal monocular performance averaged across the eyes.

Left esotropes: Deviating eye versus left eye of normal group; fellow eye versus right eye of normal group

The strabismic and fellow eye of left esotropes both differed from the respective normal eyes at certain positions in the visual field (significant Group × Eccentricity × Axis × Visual Field interaction for the deviating eye, $F(3, 100) = 6.103$, $p = 0.0007$, and fellow eye, $F(3, 100) = 4.39$, $p = 0.006$. Follow-up tests indicated that deviating eye error was larger than normal on the horizontal axes at 1° eccentricity in the left visual field and at 3°, 5°, and 7° in the right visual field. Fellow eye error was larger than normal along the horizontal axes at 1°, 5°, and 7° eccentricity in the right visual field. Neither eye differed from normal along the vertical axes. Hence, the differences of both eyes against the normal group were predominantly in the right visual field (see Figure 5A, top panels).

Right esotropes: Deviating eye versus right eye of normal group; fellow eye versus left eye of normal group

The deviating eye of right esotropes also differed from the normal comparison group at certain positions

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in the visual field (significant Group × Eccentricity × Axis × Visual Field interaction for the deviating eye, $F(3, 100) = 3.4$, $p = 0.02$); however, the fellow eye did not significantly differ from normal, $F(3, 100) = 0.92$, $p = 0.44$. Error of the deviating eye was significantly larger than normal on the horizontal axes at 5° and 7° in the left visual field (plus a marginally significant difference at 3°, $p = 0.06$), in contrast with left esotropes where the main differences were found in the right visual field. Neither eye differed from normal along the vertical axes (see Figure 5A, bottom panels).

These results suggest that the strabismic groups showed more x compression than normal in a hemifield that differed between groups. Specifically, left esotropes showed more compression in the right periphery, and right esotropes showed more compression in the left periphery. Fellow eye performance showed the same broad pattern overall, but was closer to normal for the right esotropes. The analyses below examine whether the left and right esotropes differed from each other.

Deviating eye versus fellow eye monocular performance

To evaluate the differences between eyes across groups, the variables Eye (strabismic vs. fellow; within subjects) and Strabismus Direction (left vs. right; between subjects) were included with Eccentricity, Axis, and Visual Field in a mixed repeated-measures ANOVA. Figure 5A suggests that the sign of the error of the deviating eye, but not the fellow eye, differed between groups. This effect was confirmed with a significant Strabismus Direction × Eye interaction, $F(1, 8) = 12.941$, $p = 0.007$. The deviating eye of left esotropes showed a negative (leftward) shift relative to the fellow eye on average across all locations (strabismic vs. fellow eye: −0.24 vs. 0.008°), whereas the deviating eye of right esotropes showed a positive (rightward) shift relative to the fellow eye (0.20° vs. −0.03°). Hence, the deviating eye maps of the two groups were displaced in opposite directions, unlike the fellow eye maps, which were centered.

The two groups also differed between visual fields as a function of eccentricity: significant Strabismus Direction × Eccentricity × Visual Field interaction, $F(3, 200) = 4.43$, $p = 0.005$, with the differences between groups greater in the right peripheral visual field than in the left visual field, on average over axes and eyes. The effects of visual field are explored further below.

Figure 5B shows the data in Figure 5A, with visual field recoded according to strabismus direction. For left esotropes (rightward deviation), the right visual field is termed the *leading visual field*, and the left visual field is termed the *trailing visual field*. For right esotropes, the fields are reversed (the left visual field is the leading visual field). Hence, Strabismus Direction is implicit in Visual Field recoded this way. Additionally, positive error denotes a shift toward the leading field for both groups, and negative error a shift toward the trailing visual field (i.e., the sign of the error was reversed for right esotropes). Within this framework, a shift toward the leading or trailing field in both visual fields would indicate a translation of the map toward the given field. A leading shift in the leading field, combined with a trailing shift in the trailing field, would indicate an expansion of response coordinates on both sides. A leading shift in the trailing field combined with a trailing shift in the leading visual field would indicate a compression of response coordinates, which is what we show here.

In monocular viewing, the deviating eye maps of both groups were translated toward the trailing visual field (i.e., toward the temporal visual field), on both axes, whereas the fellow eye maps were not (compare solid and dashed traces in Figure 5B). This difference between eyes was significant: significant main effect of Eye, $F(1, 8) = 12.94$, $p = 0.007$, and consistent with the Strabismus Direction × Eye effect reported earlier. On the horizontal axes, x compression increased with eccentricity in both visual fields, whereas on the vertical axes there was a slight uniform expansion in the trailing visual field. This opposing pattern of x error on the two axes was confirmed by a significant interaction between Eccentricity, Axis, and Visual Field, $F(3, 200) = 27.95$, $p < 0.0001$. Note that the opposing direction of error on the two axes is consistent with the normal pattern, and with the angular repulsion effects shown in Figures 3 and 4.

To compare compression across groups, eyes and visual fields, the data were further simplified by calculating a compression score for each subject. Compression was calculated as the difference between error at 1° and 7° eccentricity in each visual field, separately for the two axes. This value is proportional to the slope of error against eccentricity, with large values corresponding to a steeper slope, or more compression. The sign of the compression score in the trailing visual field was reversed; hence, all positive values denote compression of the response distance between 1° and 7° (i.e., larger overshooting in the center, and undershooting in the periphery), and negative values denote expansion of the same distance.

An analysis of variance on the compression score for the horizontal axes, with Strabismus Direction, Eye, and Visual Field as factors, confirmed that the amount of compression was larger in the leading visual field than in the trailing visual field for both groups. Compare the slopes of the gray versus white symbols in Figure 5B, which show a significant main effect of Visual Field: $F(1, 8) = 12.31$, $p = 0.007$; mean compression leading versus trailing: 1.30° versus 0.75°. Furthermore, compression was greater in the deviating eye than in the fellow eye for both groups. Compare the

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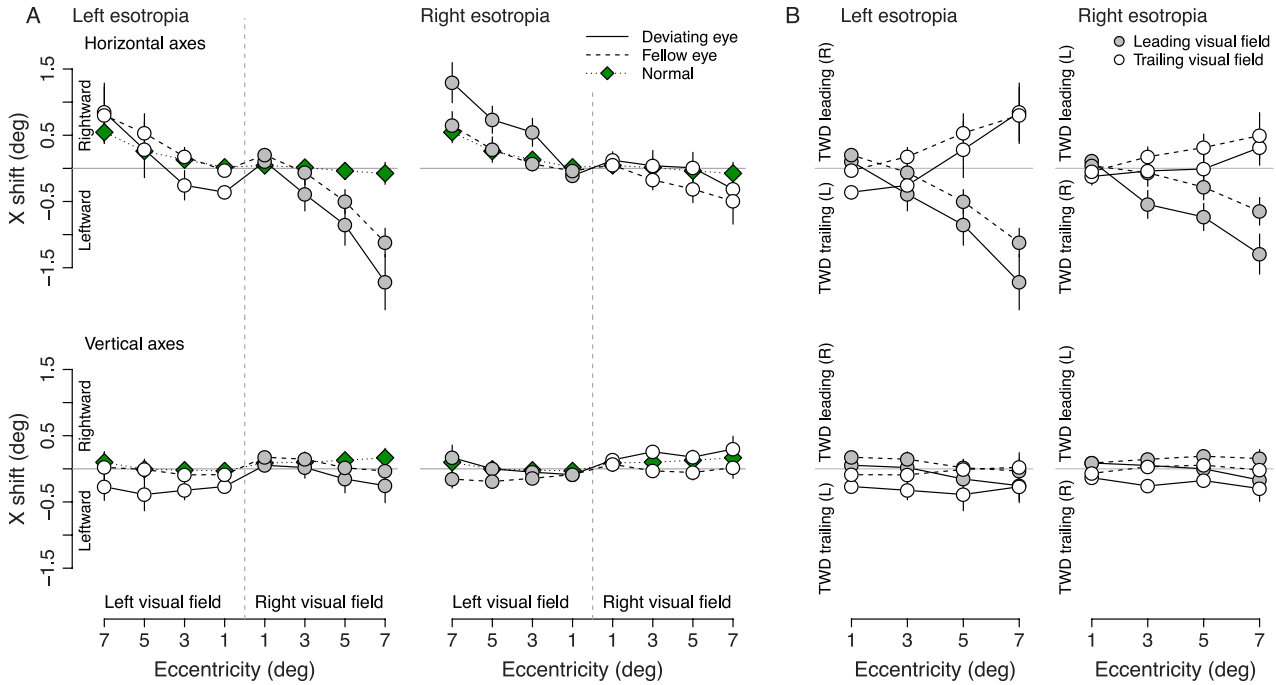


Figure 5. (A) Monocular performance of left esotropes ($N = 5$) and right esotropes ($N = 5$) shown separately for the deviating eye (solid lines) and fellow eye (dashed lines) alongside normal monocular performance averaged over the left and right eye ($N = 7$; green symbols, same data for the two strabismic groups). Top versus bottom: Horizontal versus vertical axes. Sign of error corresponds to rightward versus leftward shift as in previous figures. B. Data in (A) replotted with visual fields recoded as leading (gray symbols) and trailing (white symbols) for both groups. Leading visual field is the right visual field for left esotropia, left visual field for right esotropia (see text for explanation). Sign of error denotes shift toward leading or trailing visual field. Error bars show the standard error of the mean.

slopes of solid versus dashed traces in Figure 5B, which show a significant main effect of Eye: $F(1, 8) = 8.68$, $p = 0.01$ (mean compression strabismic versus fellow eye: 1.21° vs. 0.85°). Although Figure 5 suggests that the visual field difference in compression may have been larger for the deviating eye than for the fellow eye, this effect did not achieve significance: Eye × Visual Field interaction, $F(1, 8) = 2.875$, $p = 0.13$. The main effect of Strabismus Direction was not significant, $F(1, 8) = 1.94$, $p = 0.20$, and Strabismus Direction did not interact significantly with Eye and Field ($p > 0.05$ all interactions), confirming that left esotropes and right esotropes showed the same pattern. The compression scores of the strabismic and fellow eye were positively correlated in the leading visual field, $r = 0.84$, $t(8) = 4.32$, $p = 0.002$, in the trailing visual field, $r = 0.60$, $t(8) = 2.12$, $p = 0.06$, and on average across the two visual fields, $r = 0.84$, $t(8) = 4.37$, $p = 0.002$.

A similar analysis on the vertical axes indicated a marginally significant interaction between Eye and Visual Field, $F(1, 8) = 3.76$, $p = 0.088$, with the mean effects suggesting a difference in the compression score between visual fields for the deviating eye (leading vs. trailing: 0.28° vs. −0.08°), but not the fellow eye (leading vs. trailing: 0.07° vs. 0.08°). Here, as well, the compression scores of the strabismic and fellow eye were positively correlated in the leading visual field, $r = 0.74$, $t(8) = 3.11$, $p = 0.01$; the trailing visual field, $r = 0.61$, $t(8) = 2.19$, $p = 0.059$; and on average across the two fields, $r = 0.86$, $t(8) = 4.85$, $p = 0.001$.

Overall, these results confirm that the deviating eye map was shifted toward the trailing visual field, and x compression was larger than normal in the leading visual field. Compression was larger in the deviating eye than the fellow eye, but the visual field difference in compression did not differ between the eyes.

Strabismic group: Dichoptic performance

Figure 6 shows dichoptic performance of thirty subjects grouped by esotropia or exotropia of the left or right eye. Figure 6A shows that the entire positional map was shifted leftward or rightward, depending on strabismus direction. Responses of right esotropes and left exotropes were shifted leftwards, consistent with the perceived leftward displacement of the response probe relative to its true position, and vice versa for left esotropes and (less so) right exotropes (see Figure 1 for details). Positional maps of left esotropes were essentially the reverse of right esotropes. Furthermore, right esotropes closely resemble left exotropes.

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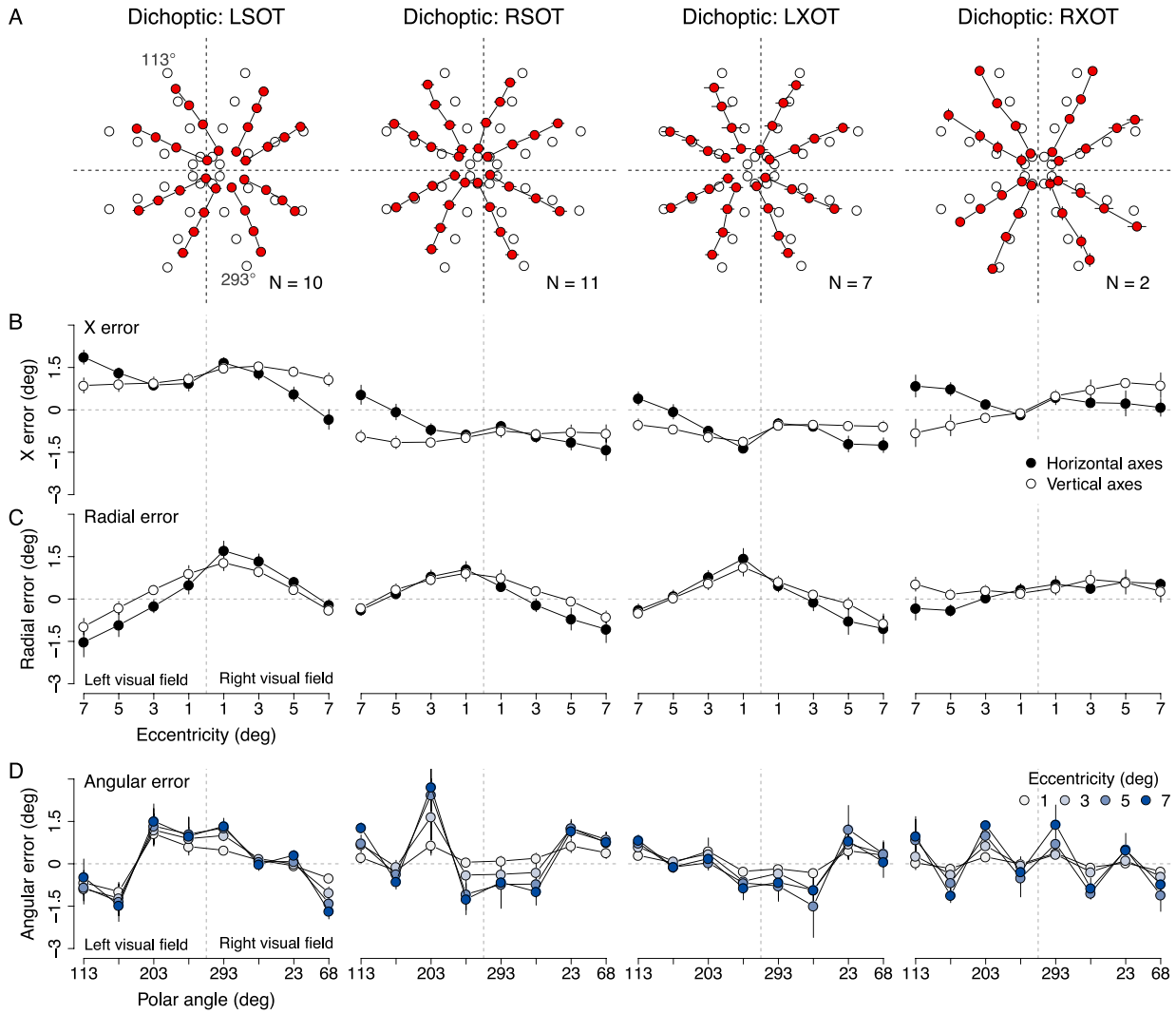


Figure 6. (A) Dichoptic positional maps of the four strabismic groups. White symbols: correct response position. Red symbols: average response position. (B–D): X error, radial error ,and angular error for the four groups, plotting convention same as in Figures 3 and 4. Error bars show the standard error of the mean.

The average signed dichoptic error across the tested locations was significantly correlated with strabismus angle, $r = 0.63$, $t(28) = 4.27$, $p = 0.0002$, confirming that the overall direction of shift corresponded to strabismus direction. However, the magnitude of the dichoptic shift (0.85° or 1.50 PD) was substantially lower than the average angle of strabismus (9.16 PD), indicating that the dichoptic shift did not match the objective angle for many subjects. Furthermore, shift magnitude was not significantly correlated with strabismus angle magnitude, $r = 0.29$, $t(28) = 1.60$, $p = 0.12$. Strabismus angle is known to vary with viewing conditions and time. Therefore, the objective angle during task performance may not have been identical to that measured by the cover test. However, the close agreement in the objective angles given by the near and far cover tests (measured at 33 cm vs. 4 m; see Table 2), and the large discrepancy between the average shift and the objective angle, suggests that the perceived visual direction of the deviating eye had shifted to minimize the discrepancy in visual directions between eyes (i.e., that retinal correspondence was anomalous rather than normal in these subjects), in addition to any variations in objective angle during the task.

Figures 6B, C, and D show that the dichoptic shift was not uniform across the visual field. Instead, the profile of the shift was similar to that measured in the monocular conditions: x and radial compression in the periphery of both visual fields, and an angular bias that varied systematically with polar angle. The angular bias appears distorted in the dichoptic condition compared to the monocular condition because of the large shift in response x coordinates; centering the data restores the pattern (centered data not shown). Overall, the monocular spatial biases were intact in the dichoptic

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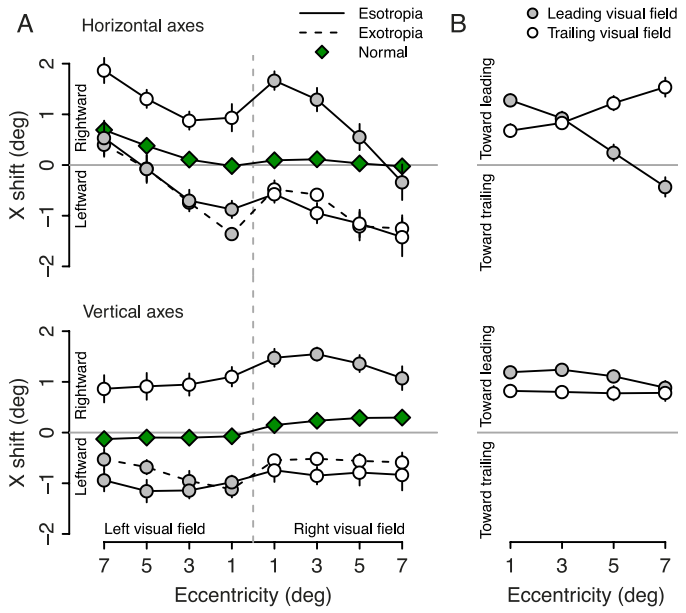


Figure 7. (A) Dichoptic performance of three strabismic groups (solid traces: esotropes; dashed traces: exotropes) shown separately for the horizontal and vertical axes. Normal dichoptic performance shown in green. Left esotropes ($N = 10$) showed a positive, rightward shift; right esotropes ($N = 11$) and left exotropes ($N = 7$) showed a negative, leftward shift. Gray versus white symbols denote leading versus trailing visual field for each group. (B) Data in (A) averaged over the three groups ($N = 28$), separately for the leading and trailing visual field. Positive values show a shift toward the leading visual field, and negative values a shift toward the trailing visual field. Error bars show the standard error of the mean, smaller than symbol where not shown.

map, and translated away from the center in a direction consistent with strabismus angle.

Figure 7A compares dichoptic performance of left esotropes, right esotropes, and left exotropes on the horizontal and vertical axes. Normal dichoptic performance is also plotted. Right exotropes were excluded because of the small sample size ($N = 2$). Thus, the figure shows the data for 28 strabismic subjects in all. Aside from the difference in the sign of error overall, the leftward and rightward deviating groups showed a symmetric pattern across the visual field on both axes, with the visual fields reversed for the leftward deviating groups (RSOT and LXOT). Right esotropes did not significantly differ from left exotropes at any location, confirmed by a separate analysis that treated Strabismus Type (esotropia vs. exotropia) as a grouping variable: The main effect of Strabismus Type was not significant, and Strabismus Type did not interact with Eccentricity, Axis, or Visual Field ($p > 0.05$ for all interactions). Hence, right esotropes and left exotropes were pooled in comparisons against left esotropes, using the grouping variable Strabismus Direction (leftward vs. rightward) for the analyses that follow.

Figure 7B shows average performance of the three groups after recoding visual field as leading versus trailing and expressing the shift accordingly. With visual field recoded as above, the groups no longer differed at any location. The main effect of Strabismus Direction was not significant, $F(1, 26) = 0.55$, $p = 0.47$, and Strabismus Direction did not significantly interact with any of the variables (separate groups not shown in Figure 7B). The dichoptic map was shifted toward the leading visual field, consistent with strabismus direction, and the shift varied substantially across visual field positions: significant interaction of Eccentricity, Axis, and Visual Field, $F(3, 260) = 33.84$, $p < 0.00001$. The pattern of error suggests that the monocular pattern of compression was intact (compare Figures 5B and 7B).

As was done for the monocular data, a dichoptic compression score was computed for every subject as the difference between X error at 7° and 1° eccentricity, separately for each visual field and axis. Large values indicate greater compression, irrespective of the translation of the positional map. The compression scores were analyzed separately for the axes, with a two-factor mixed ANOVA including Strabismus Direction and Visual Field. On the horizontal axes, the amount of compression was significantly larger in the leading visual field than in the trailing visual field. There was a significant main effect of Visual Field: $F(1, 26) = 17.48$, $p = 0.0002$; mean compression leading versus trailing = 1.70 versus 0.85°. The effect of Strabismus Direction was not significant, $F(1, 26) = 1$, $p = 0.33$, and Strabismus Direction did not interact significantly with Visual Field, $F(1, 26) = 0.66$, $p = 0.42$. A small amount of compression was evident in the leading visual field on the vertical axes. A similar analysis on the vertical data confirmed that the compression differed between visual fields, $F(1, 26) = 5.097$ $p = 0.03$; mean compression leading versus trailing, 0.31° versus −0.04°. The group difference was not significant.

These results suggest that the asymmetric compressive bias observed in the monocular conditions was present in the dichoptic map, and shifted in a direction consistent with angle of strabismus.

Strabismic group: Adjusted dichoptic error

To assess whether the variation in the dichoptic shift was fully accounted for by the monocular effects, we computed the difference between the dichoptic error and the monocular error of the deviating eye for ten subjects who performed the task in both conditions. Figure 8 shows the dichoptic and monocular data pooled across five left esotropes and five right esotropes (same subjects as in Figures 4 and 5), alongside the

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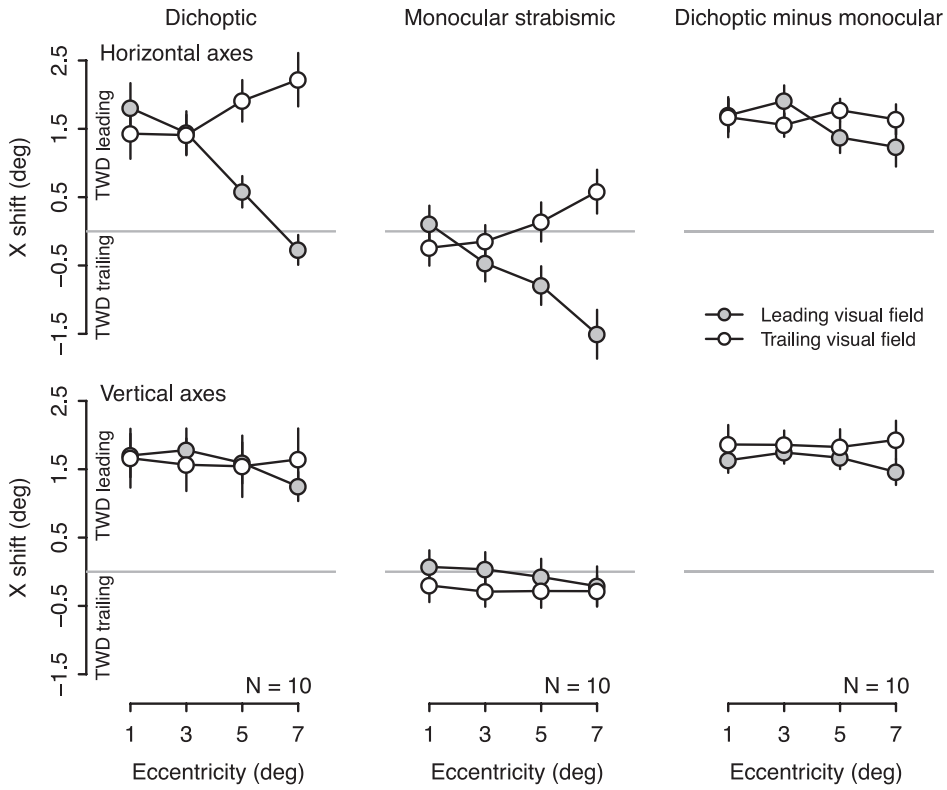


Figure 8. Difference in *x* shift between the dichoptic and monocular conditions for a subset of subjects who performed the task in both conditions (five left esotropes, five right esotropes; same subjects as in Figures 4 and 5). Left: Dichoptic data. Middle: Monocular data from the deviating eye. Right: Difference in error between the dichoptic and monocular conditions. Gray versus white symbols: leading versus trailing visual field for both groups. Top versus bottom panels: Horizontal versus vertical axes.

difference measure, here termed the adjusted shift. Plotting convention is the same as in Figures 5 and 7. If the variation in dichoptic error shown in Figure 5 was produced solely by the effects present in monocular viewing, the adjusted shift should be constant across the visual field. Any nonuniformity in the adjusted shift indicates an additional source of error.

Figure 8 shows that the pattern of dichoptic error (left panel) for this subset of ten subjects was similar to the pattern of the full group of twenty-eight subjects shown in Figure 7. The monocular pattern (middle panel) is simply the average of the deviating eye data shown in Figure 5, and is much like the dichoptic condition. The adjusted shift (Figure 8, right), was 1.7° toward the leading visual field on average across all points, and varied with visual field position, confirmed by a significant interaction between Eccentricity and Visual Field, $F(3, 80) = 4.59$, $p = 0.005$. The interaction of Axis, Eccentricity, and Visual Field approached significance, $F(3, 80) = 1.82$, $p = 0.15$. On the horizontal axes, the adjusted shift varied with visual field position: significant Eccentricity × Visual Field interaction, $F(3, 24) = 3.24$, $p = 0.03$, with a significant effect of eccentricity in the leading visual field, $F(3, 24) = 3.51$, $p = 0.03$, but not the trailing visual field, $F(3, 27) = 0.26$, $p = 0.85$. Post hoc tests indicated that the adjusted shift in the leading field differed between 3° and 5° eccentricity (0.54° difference), and 3° and 7° eccentricity (0.67° difference). The other pairwise eccentricity differences were not significant. The pairwise differences between visual fields at each eccentricity did not achieve significance at any eccentricity. On the vertical axes, the adjusted shift did not differ between visual fields or eccentricities; however, the interaction between Eccentricity and Visual Field approached significance, $F(3, 24) = 1.90$, $p = 0.15$.

Overall, the adjusted dichoptic shift varied with visual field position only in the leading visual field on the horizontal axes. The direction of variation was consistent with a slight additional compression between 3° and 7° in the leading visual field, beyond that found in the monocular condition. As with the monocular and dichoptic conditions, a compression score was calculated for the adjusted shift as the difference between error at 7° and 1° eccentricity separately for the visual fields and axes. The compression score did not differ significantly between visual fields either on the horizontal axes, $t(9) = 0.91$, $p = 0.38$), or on the vertical axes, $t(9) = 0.25$, $p = 0.81$.

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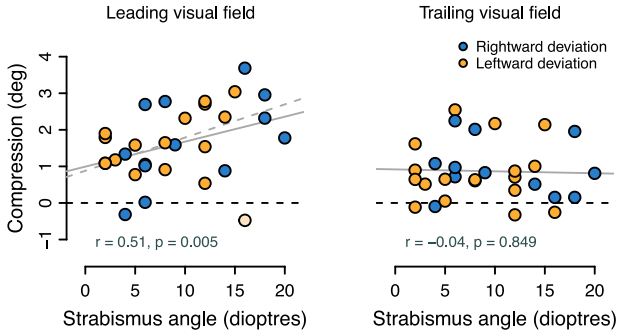


Figure 9. Scatterplots of the dichoptic compression score of each subject (horizontal axes only) against angle of strabismus in prism diopters, measured by the near cover test. Compression was calculated as the difference between *x* error at 7° and 1° eccentricity. Positive values indicate compression of distance between responses at 1° and 7°, irrespective of the overall shift of response coordinates; negative values indicate expansion. Blue versus orange symbols: rightward versus leftward ocular deviation. Leading visual field = right visual field for subjects with rightward deviation, left visual field for subjects with leftward deviation. Line of best fit shown in gray. Correlation statistics (Pearson's *r* and *p* value) shown in each plot. One subject in the horizontal-leading condition (left plot) was a significant outlier (light orange symbol below line of zero compression) and was excluded from the correlation statistic (solid vs. dashed gray lines show fit with and without outlier).

These results suggest that there was a slight additional compression in the dichoptic condition, but the bulk of the variation in the dichoptic shift could be attributed to the compressive effects found in monocular conditions.

Association of compression with strabismus angle

Figure 9 shows the dichoptic compression score of individual strabismic subjects against angle of strabismus. There was a positive correlation between the compression score and strabismus angle on the horizontal axes in the leading visual field ($r = 0.51$, $p = 0.005$; top left panel of Figure 9). The slope of the best linear fit of compression to strabismus angle was 0.09, i.e., an increase in compression of about a tenth of a degree per unit increase in angle of strabismus, or half a degree for every five prism diopters. The compression score was not significantly correlated with strabismus angle in the leading visual field on the vertical axes, or in the trailing visual field on either axis.

Prism-induced shift in normal subjects

To assess whether the compression shown in dichoptic viewing by the strabismic group could be induced in normally aligned individuals by translation of the image in one eye, a subset of normal subjects

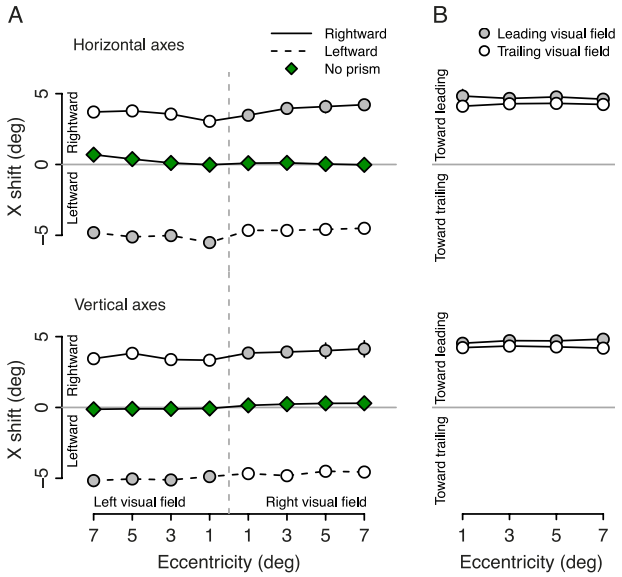


Figure 10. Prism control: Normally aligned subjects performed the task with a base-in prism of 12–13 diopters placed in front of one eye, to induce a leftward shift ($N = 4$) or a rightward shift ($N = 2$). (A) *X* error against eccentricity for rightward and leftward groups plotted alongside normal (no-prism) dichoptic controls, shown in green; same data as in Figure 7A. Top versus bottom: Horizontal versus vertical axes. (B) *X* error plotted against eccentricity, with visual field recoded as leading versus trailing, as was done for the strabismic groups. Error bars represent standard error, smaller than symbol where not shown.

performed the task with a base-in prism of 12–13 diopters in front of one eye. A base-in prism displaces the image temporally on the screen, resulting in a compensatory nasalward response (similar to exotropia). Six subjects performed the task with a prism (four were induced with a leftward shift), at a viewing distance of 57 cm. A closer viewing distance was used than in the previous conditions because the screen size at 114 cm could not accommodate the perceived translation of the image at 12–13 diopters (subjects adapted to prism angles lower than 10 diopters; hence, larger angles were used). Figure 10 shows performance of these subjects using the same convention as Figures 5 and 7. Note the much larger scale compared to the strabismic-dichoptic group (5° shift vs. 2°). The control subjects showed a uniform profile of error against eccentricity, with a slight but consistent increase in error in the leading visual field over the trailing visual field, $F(1, 5) = 31.3$, $p = 0.003$, and negligible compression on either axis in either visual field. These data suggest that the pattern of compression shown by strabismic subjects was associated with long-standing ocular misalignment, and not with artifacts arising from the translation of the image in one eye.

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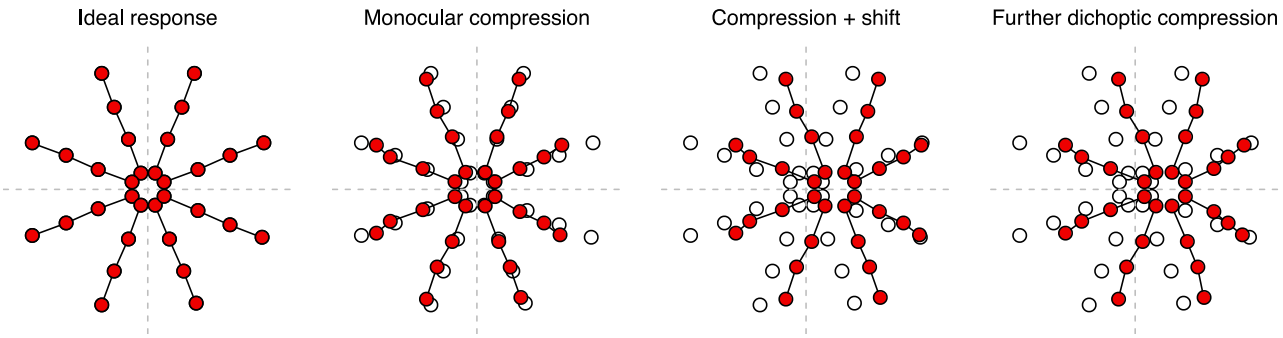


Figure 11. Simulated dichoptic map for a left esotrope. Left: Ideal positional map, zero error at all locations. Second from left: Monocular compression applied to ideal responses based on data from left esotropes (Figure 5B; deviating eye); note greater compression in leading visual field (right) than trailing visual field (left). A small amount of compression was also applied to *y* coordinates. Third from left: Uniform shift of 1.7° added to monocularly compressed map to produce dichoptic map. Far right: Final map includes additional dichoptic compression (calculated from adjusted dichoptic shift; see Figure 8A).

Discussion

The constant horizontal error in a positional localization task was measured at multiple positions in the visual field of strabismic subjects with varying degrees of ocular misalignment, and in a normal control group, to map positional accuracy in monocular and dichoptic viewing conditions. In monocular viewing, the constant error measures spatial bias at a given position. In dichoptic viewing, the constant error of strabismic subjects reflects the perceived shift of the stimulus imaged on the deviating eye in addition to any spatial bias (Figure 1). Although the biases on this task are well described in polar coordinates, the perceived shift in strabismus is primarily in the horizontal direction—hence, the use of Cartesian *x* error. The focal question was whether the strabismic dichoptic shift is uniform in the extrafoveal visual field, and whether the nonuniformities if any, exceed baseline monocular biases. A pattern of overshooting at central locations combined with undershooting in the periphery was termed compression, i.e., of the distance between central and peripheral response coordinates. The term compression as used here applies to response locations, distinct from the spatial representation. Since the task called for localization with respect to a reference in the opposite hemifield, the compression could reflect distortions in either hemifield. Despite a great deal of heterogeneity in individual positional maps (see Figure 2), virtually all subjects showed the compressive biases described here.

In normal subjects, the left peripheral hemifield was compressed (Figure 3). In strabismic subjects, both hemifields were compressed, and compression was larger in the visual field in the direction of ocular deviation (nasal visual field of esotropes and temporal visual field of exotropes), here termed the leading visual field (Figures 4 and 5). Unlike the *x* error compression on the horizontal axes alone, radial compression was evident on both axes. Therefore, the axis-specific *x* compression is better understood as a global radial compression, driven by *x* error on the horizontal axes and *y* error on the vertical axes. The hemifield-specific effects on compression were present in radial error (Figures 4 and 6). Thus, the asymmetric visual field compression did not depend on the measure used.

In monocular conditions, compression was stronger in the deviating eye than in the fellow eye (Figure 5), and the deviating eye map showed an unexpected translation in the direction against strabismus angle (toward the trailing visual field). The dichoptic map was shifted in the direction expected by strabismus angle, with the monocular compression pattern intact (Figures 6 and 7). Hence, the dichoptic shift did vary with visual field position, but the variation in shift was largely accounted for by the monocular pattern (Figure 8). This result is summarized in Figure 11. The dichoptic map for a subject with left esotropia is shown as the sum of an asymmetric monocular bias and a rightward translation of the entire map. These two components are sufficient to reproduce the pattern shown for left esotropes in Figure 6. The average dichoptic shift was not significantly correlated with strabismus angle, but the amount of compression was (Figure 9). The strabismic pattern of compression could not be reproduced dichoptically in normal subjects by misaligning the visual inputs with a prism, suggesting that the strabismic pattern was produced by long-standing ocular misalignment (Figure 10).

Asymmetric visual field compression

The response compression in both visual fields arose from a pattern of error in which subjects overshot central targets and undershot peripheral targets, with best accuracy at 3° eccentricity, near the median location in each visual field. Bedell and Flom (1981) also reported an overestimation of small spatial extents

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combined with underestimation of large extents in partitioning judgments of strabismic subjects. The simplest interpretation of these patterns is a regression to the mean of the stimulus sample (here, the midpoint within each visual field), observed in a variety of spatial, temporal, and cognitive judgments (Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Hollingworth, 1910; Huttenlocher, Hedges, & Duncan, 1991; Jazayeri & Shadlen, 2010; Mansouri, Hansen, & Hess, 2009) Although we did not test this here using variable median stimulus contexts, the broad resemblance between the normal and strabismic bias suggests that the compression itself is of less interest than the visual field asymmetries associated with strabismus angle. The normal compression was also asymmetric, however. This finding is consistent with a normal overestimation of left visual space shown by Bedell and Flom (1983). Their data and ours indicate that it is the left visual field, and not the nasal or temporal visual field of either eye that is overestimated in normal subjects, in contrast with the Kundt partition effect in which the nasal spatial extent is overestimated. The effect found here may be related to the phenomenon of pseudoneglect, a similar overestimation of leftward spatial extents attributed to hemispheric differences in spatial attention (e.g., Jewell & McCourt, 2000; McCourt & Jewell, 1999).

In strabismic subjects, we found a reliable pattern of response compression in the leading visual field, which is the nasal visual field of esotropes, and the temporal visual field of exotropes. Similar visual field asymmetries in strabismic spatial judgments have been reported previously in monocular tasks. Bedell et al. (1985) reported that the constant error of monocular alignment varied with direction of ocular deviation. In their study, alignment errors were temporalward in 17 of 20 esotropes, and nasalward in two of three exotropes (i.e., toward the trailing visual field for both groups), unlike normal subjects who showed equal error in both directions. This asymmetry was not present in partitioning judgments (Bedell & Flom, 1981). Fronius and Sireteanu (1989) reported the opposite result in a smaller number of subjects—temporalward alignment errors for exotropes and nasalward errors for esotropes. The differences between these studies may lie in the methods (e.g., constant stimuli vs. adjustment) and other procedural factors. Sireteanu and Fronius (1981) also found nasotemporal asymmetries in visual acuity, with worse acuity in the nasal retina or temporal visual field of esotropes (i.e., the trailing visual field), associated with a regional difference in the depth of interocular suppression. Nasotemporal asymmetries of motion pursuit also have been reported (Kiorpes, Walton, O'Keefe, Movshon, & Lisberger, 1996; Tychsen & Lisberger, 1986), however these relate to the direction of motion rather than the visual field in which the motion appears. These previous studies have linked the spatial distortions to visual acuity in strabismus, but have not shown an association between distortion and strabismus magnitude. The correlation between the compression score and strabismus angle shown here suggests a visual field specific adaptation to the ocular misalignment. This combined with the absence of a correlation between mean shift magnitude and strabismus angle suggests that this adaptation is independent of the state of retinal correspondence of the subject.

Deviating eye versus fellow eye

The fellow eye has been found to share the anomalies of the deviating eye on certain spatial tasks (Economides, Adams, & Horton, 2016; Kandel, Grattan, & Bedell, 1980; Kelly, Chino, Cotter, & Knuth, 1997). Here, the strabismic and fellow eye showed similar compressive biases overall, but differed in several respects.

The deviating eye map was shifted toward the trailing visual field, unlike the fellow eye map, which was centered (Figure 5), and unlike the dichoptic map, which was shifted toward the leading visual field (Figure 7). While the dichoptic shift was in the expected direction, there is no obvious explanation for the monocular shift of the deviating eye map in the opposite direction to the dichoptic map. The habitual state of misalignment is altered in monocular viewing, with the deviating eye fixating more centrally when the fellow eye is closed. This change in the resting position of the eye may induce a shift of spatial coordinates (or response coordinates), in the direction opposite to the habitual state. Such a shift is not easily predicted from eccentric fixation of the deviating eye, characteristic of certain strabismic individuals in monocular viewing. For subjects with eccentric fixation performing the task, the target and response dots would lie at unequal distances from the anatomical fovea, with the fixation cross imaged at an eccentric retinal location. In these conditions, subjects would presumably judge stimulus distance against the fixation cross regardless of its retinal location. If subjects were biased by relative stimulus distance from the fovea, and adjusted the response probe to equate or compensate for this distance, a leading shift should arise at all tested locations (similar to the dichoptic case), and not the trailing shift in one visual field observed here. However, eccentric fixation could produce additional biases not considered above.

In the comparisons of both eyes against the normal groups, left esotropes and right esotropes differed in the pattern shown (Figure 5A). For left esotropes, both the deviating eye and the fellow eye differed from normal in the leading peripheral visual field where

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compression was strongest (i.e., fellow eye performance was also anomalous in this region). For right esotropes, only the deviating eye differed from normal in the leading field. The difference against normal was easier to establish for left esotropes, because the normal group showed negligible compression in the right visual field (leading visual field of left esotropes), but measurable compression in the left visual field (leading visual field of right esotropes). Had the normal group shown a symmetric pattern (of either equal or negligible bias in both visual fields), the fellow eye of both groups would have compared similarly.

In the within-group comparisons between the strabismic and fellow eye, the fellow eye showed less compression than the deviating eye overall, but the same difference in compression between the leading and trailing visual field that was found for the deviating eye. Although the data suggest that the visual field difference in compression was not as large for the fellow eye as the deviating eye, this difference between eyes did not achieve significance. The compression in both visual fields was strongly correlated between eyes, suggesting that performance through both eyes was affected by a common mechanism.

Dichoptic shift and relationship with retinal correspondence

One of the goals of this study was to examine whether the diplopic shift of the image in the deviating eye is uniform across the visual field, independently of spatial distortions that may exist otherwise. In clinical methods where subjects superimpose targets dissociated between the eyes (e.g., Hess screen test, Lancaster red-green test, see von Noorden et al., 2002) the perceived shift provides a measure of retinal correspondence. Below, we consider the relationship between retinal correspondence and performance on this task.

The sign of the average dichoptic shift across the locations tested here was consistent with the sign of the objective angle of strabismus. However, the size of the average shift was smaller than the average objective angle (1.5 vs. 9 PD), and uncorrelated with objective angle. No subject showed a shift equal to the objective angle (i.e., normal retinal correspondence). In other words, the data from all subjects suggested some degree of anomalous retinal correspondence, primarily of the unharmonious type (UHARC). The prevalence of anomalous retinal correspondence (and UHARC especially), is disputed in the clinical literature, because the result depends greatly on how the eyes are dissociated, or how closely the viewing conditions resemble casual seeing (Bagolini, 1981; Burian, 1947; Daum, 1982; Jennings, 1985; Maraini & Pasino, 1964; Travers, 1938; von Noorden & Campos, 2002). It has been suggested that anomalous retinal correspondence is more likely for small angle strabismus (Bagolini, 1981; Jennings, 1985; Wong, Lueder, Burkhalter, & Tychsen, 2000), where the image disparity is within tolerance of binocular receptive fields in extrastriate cortex (10° or 18° PD; Shlaer, 1971; Campos, 1980; Cynader, Gardner, & Mustari, 1984; Grant and Berman, 1991, but also see Wong et al., 2000 for different limits). By this account, there is no shift in the native retinal coordinates for large angle strabismus (>20 PD), outside the range tested in this study. In certain types of strabismus, retinal correspondence is influenced by changes in vergence and accommodation, which were not varied here. Furthermore, the viewing distance used for the task (114 cm) differed from the distance at which the objective angle of deviation was determined (≈100 cm). A combination of these factors may account for our finding that the subjective shift was smaller than the objective angle for the majority of subjects tested.

There is mixed evidence for regional variation in retinal correspondence. Measurements of the subjective angle outside the fovea have shown it to be uniform (Kretzschmar, 1955), to covary with the regional extent of interocular suppression (Travers, 1938), and to vary with target eccentricity (Burian, 1941; Flom, 1980; Sireteanu & Fronius, 1989). Burian (1941) discerned two broad patterns of retinal correspondence: normal correspondence in the central visual field coupled with anomalous fusion in the periphery, and the reverse, in addition to transitional patterns between the two. Flom's (1980) horopter measurements in strabismic subjects showed a central notch in the horopter in addition to peripheral horopter deformations, consistent with normal correspondence near the center of gaze and anomalous correspondence in the periphery. Sireteanu and Fronius (1989), reported findings consistent with Flom's (1980) horopter data for a subset of strabismic subjects using a method similar to that used here.

We found that the dichoptic shift did vary in the extrafoveal visual field, but that the pattern of variation was no different than that found in monocular viewing. The monocular data showed a peripheral compression that was more pronounced in the leading visual field than in the trailing visual field. The same pattern was present in the dichoptic data, translated away from the central coordinates in a direction consistent with strabismus angle. The adjusted dichoptic shift, i.e., the dichoptic shift corrected for the monocular effects, showed a slight additional variation on the horizontal axes in the leading visual field (Figure 8), but this effect was negligible compared to the monocular bias. The negligible residual variation in dichoptic error suggests that variations in retinal correspondence, if any, did not manifest here. On the other hand, the biases measured here in monocular and dichoptic conditions

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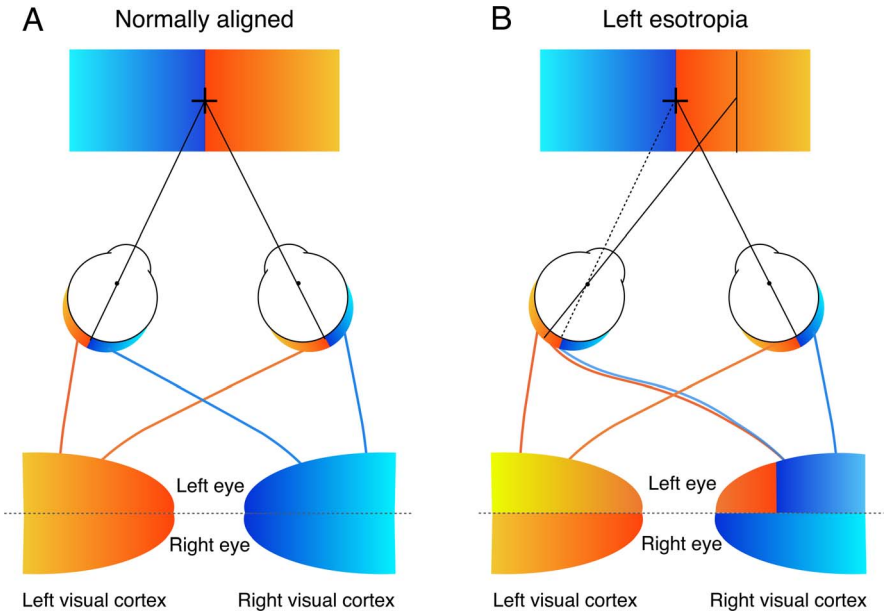


Figure 12. Schematic retinal and cortical representation of binocular visual input for normal visual alignment (A), and strabismus (left esotropia; B). Color gradient shows eccentricity, not adjusted for cortical magnification. Inward turn of the left eye results in right visual field projecting to nasal retina and right visual cortex. Entire cortical map of left eye input is shifted relative to the right eye.

may affect measurements of binocular correspondence made using related methods.

Cortical representation

The amblyopic visual deficits that frequently accompany strabismus have been linked to a number of subcortical and cortical anomalies (Anderson & Swettenham, 2006; Barnes, Hess, Dumoulin, Achtman, & Pike, 2001; Hess, Thompson, Gole, & Mullen, 2010). Spatial localization deficits have been attributed to a change in the grain of cortical sampling (Hussain et al., 2015; Klein & Levi, 1987; Levi, Klein, & Yap, 1987), miscalibration of cortical inputs (Clavagnier, Dumoulin, & Hess, 2015; Hess & Field, 1994), and connective anomalies within and across successive cortical layers (Li, Mullen, Thompson, & Hess, 2011; Yu & Levi, 1998). These accounts have primarily been applied to threshold measurements, but may encompass spatial biases such as those reported here. The above cortical changes would presumably be engendered by a change in binocular spatial coding due to the ocular misalignment, affecting monocular and binocular judgments, both. Therefore, it is worth considering whether changes in the topography of binocular visual input might account for or subsume some of these effects.

Based on horopter measurements in strabismic subjects, Flom (1980) proposed alterations in retinal correspondence in esotropia associated with functional connections between opposite cortical hemispheres, also suggested by others (e.g., Burian, 1951; Gupta et al., 2016; Tyler, 2004). Such a situation is shown schematically in Figure 12 for a left esotrope. The projection of the right visual field via nasal retinal input to right visual cortex implies a change in the overall retinotopic mapping of the deviating eye in occipital cortex or elsewhere. The evidence for such retinotopic remapping in strabismus is mixed (Conner, Odom, Schwartz, & Mendola, 2007; McCormack, 1990). McCormack (1990) found identical visual evoked potential (VEP) topographies from stimulation of the anatomic foveae, and different topographies from stimulation of noncorresponding points of strabismic subjects, indicating that the native positional encoding mechanisms in strabismic cortex were undisturbed. However, Conner et al. (2007), using fMRI, found a shift in the cortical topography of the amblyopic eye relative to the fellow eye in dichoptic viewing, i.e., the same cortical region represented the fovea of the fellow eye and parafoveal visual field of the deviating eye. Further work is needed to confirm such cortical remapping in strabismus, and to clarify its effects on the sense of position in monocular and binocular viewing.

Summary and conclusions

The constant error of strabismic subjects in monocular and dichoptic positional judgments revealed an asymmetric spatial bias that could be summarized as a

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compression of response coordinates, exaggerated in the visual field in the direction of ocular deviation. The magnitude of dichoptic compression was correlated with strabismus angle. The monocular pattern of compression accounted for the variation in dichoptic judgments, suggesting that binocular correspondence in these strabismic subjects was uniform in the extrafoveal region up to 7° eccentricity. The asymmetric compressive bias appears to arise from prolonged ocular misalignment, and may arise from a cortical adaptation to strabismus that differs between the visual fields.

Keywords: bias, *bisection*, *alignment*, *fusion*, *amblyopia*, *diplopia*, *horopter*, *suppression*, *binocular*, *retinal correspondence*, *reference repulsion*

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References

Anderson, S. J., & Swettenham, J. B. (2006). Neuroimaging in human amblyopia. *Strabismus*, *14*(1), 21–35.

Bagolini, B. (1974). Sensory anomalies in strabismus. *British Journal of Ophthalmology*, *58*(3), 313–318.

Bagolini, B. (1982). Anomalous fusion. In A. T. M. van Balen, W. A. Houtman (Eds.), *Documenta Ophthalmologica Proceedings Series: Strabismus Symposium* (Vol. *32*, pp. 41–52). Amsterdam, the Netherlands: Springer.

Barnes, G. R., Hess, R. F., Dumoulin, S. O., Achtman, R. L., & Pike, G. B. (2001). The cortical deficit in humans with strabismic amblyopia. *The Journal of Physiology*, *533*(Pt 1), 281–297.

Bedell, H. D., & Flom, M. C. (1981). Monocular spatial distortion in strabismic amblyopia. *Investigative Ophthalmology Vision Science*, *20*(2), 263–268. [PubMed] [Article]

Bedell, H. E., & Flom, M. C. (1983). Normal and abnormal space perception. *American Journal of Optometry and Physiological Optics*, *60*(6), 426–435.

Bedell, H. E., Flom, M. C., & Barbeito, R. (1985). Spatial aberrations and acuity in strabismus and amblyopia. *Investigative Ophthalmology Vision Science*, *26*(7), 909–916. [PubMed] [Article]

Burian, H. (1941). Fusional movements in permanent strabismus—A study on the role of the central and peripheral retinal regions in the act of binocular vision in squint. *Archives of Ophthalmology*, *26*(4), 626–652.

Burian, H. (1947). Sensorial retinal relationship in concomitant strabismus. *Archives of Ophthalmology*, *37*(5), 618–648.

Burian, H. (1951). Anomalous retinal correspondence. Its essence and its significance in diagnosis and treatment. *American Journal of Ophthalmology*, *34*(21), 237–253.

Campos, E. C. (1980). Anomalous retinal correspondence. Monocular and binocular visual evoked responses. *Archives of Ophthalmology*, *98*(2), 299–302

Cicchini, G. M., Arrighi, R., Cecchetti, L., Giusti, M., & Burr, D. C. (2012). Optimal encoding of interval timing in expert percussionists. *Journal of Neuroscience*, *32*(3), 1056–1060.

Clavagnier, S., Dumoulin, S. O., & Hess, R. F. (2015). Is the cortical deficit in amblyopia due to reduced cortical magnification, loss of neural resolution, or neural disorganization? *Journal of Neuroscience*, *35*(44), 14740–14755.

Conner, I. P., Odom, J. V., Schwartz, T. L., & Mendola, J. D. (2007). Retinotopic maps and foveal suppression in the visual cortex of amblyopic adults. *The Journal of Physiology*, *583*(Pt 1), 159–173.

Cynader, M., Gardner, J. C., & Mustari, M. (1984). Effects of neonatally induced strabismus on binocular responses in cat area 18. *Experimental Brain Research*, *53*(2), 384–399.

Daum, K. M. (1982). Analysis of seven methods of determining anomalous correspondence. *American Journal of Optometry and Physiological Optics*, *59*(11), 870–877.

Demanins, R., & Hess, R. F. (1996). Positional loss in strabismic amblyopia: Inter-relationship of alignment threshold, bias, spatial scale and eccentricity. *Vision Research*, *36*(17), 2771–2794.

Economides, J. R., Adams, D. L., & Horton, J. C. (2012). Perception via the deviated eye in strabismus. *Journal of Neuroscience*, *32*(30), 10286–10295.

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Economides, J. R., Adams, D. L., & Horton, J. C. (2016). Variability of ocular deviation in strabismus. *JAMA Ophthalmology*, *134*(1), 63–69.

Flom, M. C. (1980). Corresponding and disparate retinal points in normal and anomalous correspondence. *American Journal of Optometry and Physiological Optics*, *57*(9), 656–665.

Fogt, N., Baughman, B. J., & Good, G. (2000). The effect of experience on the detection of small eye movements. *Optometry and Vision Science*, *77*(12), 670–674.

Fronius, M., & Sireteanu, R. (1989). Monocular geometry is selectively distorted in the central visual field of strabismic amblyopes. *Investigative Ophthalmology Vision Science*, *30*(9), 2034–2044. [PubMed] [Article]

Grant, S., & Berman, N. E. (1991). Mechanism of anomalous retinal correspondence: Maintenance of binocularity with alteration of receptive-field position in the lateral suprasylvian (ls) visual area of strabismic cats. *Visual Neuroscience*, *7*(3), 259–281.

Gupta, S., Kumaran, S. S., Saxena, R., Gudwani, S., Menon, V., & Sharma, P. (2016). Bold fmri and dti in strabismic amblyopes following occlusion therapy. *International Ophthalmology*, *36*(4), 557–568.

Hess, R. F., & Field, D. J. (1994). Is the spatial deficit in strabismic amblyopia due to loss of cells or an uncalibrated disarray of cells? *Vision Research*, *34*(24), 3397–3406.

Hess, R. F., Thompson, B., Gole, G. A., & Mullen, K. T. (2010). The amblyopic deficit and its relationship to geniculo-cortical processing streams. *Journal of Neuroscience*, *104*(1), 475–483.

Hollingworth, H. (1910). The central tendency of judgements. *Journal of Psychology and Scientific Methods*, *7*, 461–469.

Hussain, Z., Svensson, C.-M., Besle, J., Webb, B. S., Barrett, B. T., & McGraw, P. V. (2015). Estimation of cortical magnification from positional error in normally sighted and amblyopic subjects. *Journal of Vision*, *15*(2):25, 1–16, doi:10.1167/15.2.25. [PubMed] [Article]

Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review*, *98*(3), 352–376.

Jampolsky, A. (1955). Characteristics of suppression in strabismus. *AMA Archives of Ophthalmology*, *54*(5), 683–696.

Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience*, *13*(8), 1020–1026.

Jennings, J. A. (1985). Anomalous retinal correspondence–a review. *Ophthalmic Physiological Optics*, *5*(4), 357–368.

Jewell, G., & McCourt, M. E. (2000). Pseudoneglect: A review and meta-analysis of performance factors in line bisection tasks. *Neuropsychologia*, *38*(1), 93–110.

Johns, H. A., Manny, R. E., Fern, K., & Hu, Y.-S. (2004). The intraexaminer and interexaminer repeatability of the alternate cover test using different prism neutralization endpoints. *Optometry and Vision Science*, *81*(12), 939–946.

Kandel, G. L., Grattan, P. E., & Bedell, H. E. (1980). Are the dominant eyes of amblyopes normal? *American Journal of Optometry and Physiological Optics*, *57*(1), 1–6.

Kelly, S. A., Chino, Y. M., Cotter, S. A., & Knuth, J. (1997). Orientation anisotropy and strabismus. *Vision Research*, *37*(1), 151–163.

Kiorpes, L., Walton, P. J., O'Keefe, L. P., Movshon, J. A., & Lisberger, S. G. (1996). Effects of early-onset artificial strabismus on pursuit eye movements and on neuronal responses in area mt of macaque monkeys. *Journal of Neuroscience*, *16*(20), 6537–6553.

Klein, S. A., & Levi, D. M. (1987). Position sense of the peripheral retina. *Journal of the Optical Society of America, A*, *4*(8), 1543–1553.

Kretzschmar, S. (1955). False retinal correspondence. *Documenta Ophthalmologica Proceedings Series*, *9*(1), 46–208.

Lagrèze, W. D., & Sireteanu, R. (1991). Two-dimensional spatial distortions in human strabismic amblyopia. *Vision Research*, *31*(7–8), 1271–1288.

Levi, D. M. & Klein, S. A. (1983). Spatial localization in normal and amblyopic vision. *Vision Research*, *23*(10), 1005–1017.

Levi, D. M., Klein, S. A., & Yap, Y. L. (1987). Positional uncertainty in peripheral and amblyopic vision. *Vision Research*, *27*(4), 581–597.

Li, X., Mullen, K. T., Thompson, B., & Hess, R. F. (2011). Effective connectivity anomalies in human amblyopia. *Neuroimage*, *54*(1), 505–516.

Mansouri, B., Hansen, B. C., & Hess, R. F. (2009). Disrupted retinotopic maps in amblyopia. *Investigative Ophthalmology Vision Science*, *50*(7), 3218–3225. [PubMed] [Article]

Maraini, G., & Pasino, L. (1964). Variations in the angle of anomaly and fusional movements in cases of small-angle convergent strabismus with harmonious anomalous retinal correspondence. *British Journal of Ophthalmology*, *48*, 439–443.

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McCormack, G. (1990). Normal retinotopic mapping in human strabismus with anomalous retinal correspondence. *Investigative Ophthalmology Vision Science*, *31*(3), 559–568. [PubMed] [Article]

McCourt, M. E. & Jewell, G. (1999). Visuospatial attention in line bisection: Stimulus modulation of pseudoneglect. *Neuropsychologia*, *37*(7), 843–855.

Peirce, J. W. (2007). Psychopy–psychophysics software in python. *Journal of Neuroscience Methods*, *162*(1–2), 8–13.

Shlaer, R. (1971, August). Shift in binocular disparity causes compensatory change in the cortical structure of kittens. *Science*, *173*(3997), 638–641.

Sireteanu, R., & Fronius, M. (1981). Naso-temporal asymmetries in human amblyopia consequence of long-term interocular suppression. *Vision Research*, *21*(7), 1055–1063.

Sireteanu, R., & Fronius, M. (1989). Different patterns of retinal correspondence in the central and peripheral visual field of strabismics. *Investigative Ophthalmology Vision Science*, *30*(9), 2023–2033. [PubMed] [Article]

Sireteanu, R., Lagreze, W. D., & Constantinescu, D. H. (1993). Distortions in two-dimensional visual space perception in strabismic observers. *Vision Research*, *33*(5–6), 677–690.

Travers, T. A. (1938). Suppression of vision in squint and its association with retinal correspondence and amblyopia. *British Journal of Ophthalmology*, *22*(10), 577–604.

Tychsen, L., & Lisberger, S. G. (1986). Maldevelopment of visual motion processing in humans who had strabismus with onset in infancy. *Journal of Neuroscience*, *6*(9), 2495–2508.

Tyler, C. (2004). In W. Tasman, E. A. Jaeger (Eds.), *Binocular vision: Duane's foundations of clinical ophthalmology* (Vol. 2, Ch. 24.). Philadelphia, PA: J. B. Lippincott.

von Noorden, G. K., & Campos, E. C. (2002). *Binocular vision and ocular motility—Theory and management of strabismus* (sixth ed.). St. Louis, MO: Mosby.

Wong, A. M., Lueder, G. T., Burkhalter, A., & Tychsen, L. (2000). Anomalous retinal correspondence: Neuroanatomic mechanism in strabismic monkeys and clinical findings in strabismic children. *Journal of AAPOS*, *4*(3), 168–174.

Yu, C., & Levi, D. M. (1998). Naso-temporal asymmetry of spatial interactions in strabismic amblyopia. *Optometry and Vision Science*, *75*(6), 424–432.

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