

# Depth aftereffects mediated by vertical disparities: Evidence for vertical disparity driven calibration of extraretinal signals during stereopsis

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## Abstract

Perceptual adaptation often results in a repulsive aftereffect: stimuli are seen as biased away from the adaptation stimulus (Blakemore & Sutton, 1969). Here we report the absence of a repulsive aftereffect for a vertical gradient of vertical disparity (or vertical size ratio, VSR). We exposed observers to a binocular stimulus consisting of horizontal lines. This stimulus contains vertical, but not horizontal disparities. The visual system was able to measure the VSR of this stimulus: although the lines themselves always appeared unslanted, the VSR carried by the lines had a dramatic effect on the apparent slant of a horizontal row of dots, as predicted by recent accounts of Ogle's (1938) induced effect (e.g., Backus, Banks, van Ee, & Crowell, 1999). Yet we observed no repulsive aftereffect for the VSR signal: after adaptation to horizontal lines that were vertically larger in one eye, we found an *attractive* aftereffect, the magnitude of which was largest in stimuli that did *not* contain a VSR signal. We interpret these results as a case of recalibration: disagreement between extra-retinal eye position signals (EP) and VSR causes a recalibration in the use of EP as used in the stereoscopic perception of slant.

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**Keywords:** Binocular vision; Depth aftereffect; Vertical disparity; Adaptation

## 1. Introduction

Stereoscopic vision involves the interpretation of horizontal disparities which arise from the two eyes having different views of the same surface. Horizontal disparity can be expressed as an interocular difference in the horizontal angle subtended by a corresponding pair of points, or as a ratio of these angles (horizontal size ratio, HSR; e.g., Rogers & Bradshaw, 1993) and is the primary signal for stereoscopic depth perception. However, it is an ambiguous signal for certain tasks, one of which is slant judgment, which we shall examine here. The horizontal disparities from a surface slanted about a vertical axis at some distance in front of the observer are also produced by differently slanted sur-

faces at other combinations of distance and horizontal eccentricity with respect to the head (azimuth). Therefore, to fully specify the slant of a surface from horizontal disparities, information based on distance and azimuth of the surface is also required. Sensed eye position (EP) obtained from afferent or efferent signals is one source of this information. A second source is provided by vertical disparities, which can be expressed as an interocular difference or ratio in vertical angular subtense. The latter description is known as vertical size ratio (VSR). Together, the VSR of a surface and the horizontal gradient of VSR uniquely specify the azimuth and distance of the surface (Backus, Banks, van Ee, & Crowell, 1999; Gillam and Lawergren, 1983). Thus, estimates of stereoscopic slant can be obtained from horizontal disparities and eye position signals (HSR–EP), and also from horizontal disparities and vertical disparities (HSR–VSR). The extent to which EP and VSR are used in

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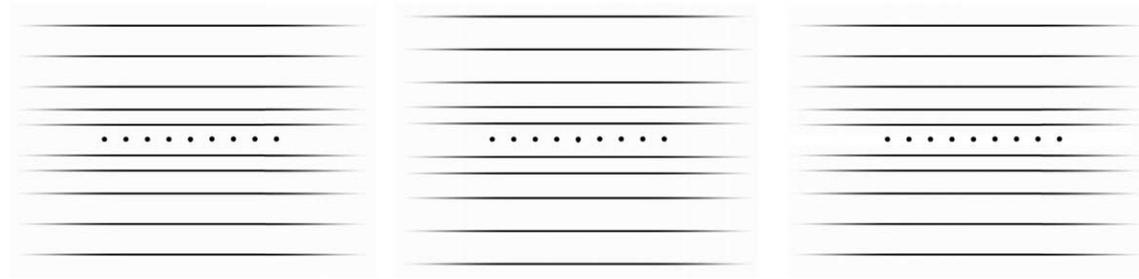


Fig. 1. Demonstration of regional use of vertical size ratio (VSR). The horizontal lines give rise only to vertical disparities. The only horizontal disparities in the display are those defined by the dot row; it has a horizontal size ratio (HSR) of 1.0. Apparent slant of the dot row depends on the VSR in the lines. Under cross fusion, two binocular (fused) images are visible, with VSR's of 1.08 and 1/1.08, respectively. The dot row appears to slant towards the eye with greater vertical size. The effect is more easily seen using a large computer display, with light elements on a black background.

stereoscopic slant perception depends on the availability of VSR information. Backus et al. (1999) found that when VSR was not available, the gain of EP signals in slant perception approached 1, and when VSR was available, EP gain was around 0.2 and VSR gain was around 0.8. The use of VSR to interpret HSR in slant perception is revealed by changes in apparent slant that result from artificially introducing a relative vertical size difference between the two eyes' images.

### 1.1. The use of vertical size ratio during stereoscopic vision

When a vertically magnifying lens is placed before the right eye, it will cause an unslanted, binocularly viewed surface to appear slanted about a vertical axis, right side near (Green, 1889; Lippincott, 1889). This phenomenon, known as the induced effect (Ogle, 1939; Backus et al., 1999), is now understood to be a corrective response to viewing geometry: objects to one side of the head are closer to one eye than the other, and the visual system uses the vertical gradient of vertical disparity (or equivalently, the VSR; Rogers & Bradshaw, 1993) within the binocular images to correct for the corresponding distortion of the horizontal disparity field (Backus et al., 1999; Gårding, Porrill, Mayhew, & Frisby, 1995; Gillam & Lawergren, 1983; Longuet-Higgins, 1982).

The visual system measures VSR by averaging vertical disparities across large (approximately  $20^\circ$ ) regions of the visual field (Adams et al., 1996; Kaneko & Howard, 1997). Horizontal disparity is represented at a much higher spatial resolution (Tyler, 1975; Westheimer & Levi, 1987); thus, the apparent depth ordering of closely spaced, horizontally separated visual features is determined by local horizontal disparities in the context of a regional VSR signal. Fig. 1 demonstrates the regional nature of VSR measurement by the visual system. Although the horizontal lines do not contain horizontal disparities, they do give rise to a VSR that can be measured by the visual system. The horizontal dot row contains horizontal disparities (in this case, zero disparities, in the distal stimulus). When the figure is cross fused, two binocularly fused images result; in the left image the lines are vertically larger in the left eye

(VSR > 1), so the dot row is perceived as slanted left side near.<sup>1</sup>

Here we ask whether the mechanism that measures VSR is susceptible to adaptation aftereffects. Reduced activity within an adapted population of VSR-sensitive neurons would be expected to produce a repulsive adaptation aftereffect, such that after adaptation to a VSR greater than 1, a test stimulus containing a VSR of 1 should appear the same as a pre-adaptation stimulus with a VSR less than 1.

A second question is whether the conflict between VSR and EP signals causes adaptation aftereffects. In principle, the visual system may recalibrate one or both signals so as to minimize persistent disagreement between them. Since VSR provides more reliable and stable information about azimuth than EP, it would make sense that EP signals should be recalibrated to be in agreement with VSR.<sup>2</sup> This eye position recalibration hypothesis predicts an *attractive* aftereffect in the case of stereoscopic stimuli within which slant must be estimated from HSR–EP alone.

### 1.2. Logic of design for current experiments

In the present study, we exposed observers to stimuli that contained various VSR values, but that did not contain horizontal disparity, and did not appear slanted (Fig. 2). We then measured the extent of VSR adaptation

<sup>1</sup> It is interesting to note in Fig. 1 that the lines remain apparently coplanar and unslanted as the dot row rotates in response to changes in VSR; thus the slant of the lines is determined by perspective cues and the visual system evidently chooses not to interpret them as lying on a common surface with the dot row. The lines have indeterminate depth and are seen as sometimes behind, and sometimes in front of the dot row, but always unslanted.

<sup>2</sup> Here, we use the term *reliability* to mean the reciprocal variance of an estimator (after Backus & Banks, 1999). We use the term *stability* to mean the reciprocal change in the bias of an estimator, per unit time. Stability thus indicates the rate that a signal drifts. An estimator may be reliable, but unstable, though the two statistics may not be independent. Note that if drift occurs whilst reliability is being estimated, then drift will add to estimator variance, i.e., reliability could reflect stability to some extent. In theory, measures of estimator reliability and stability can be used to determine the extent to which an estimator should be recalibrated (Backus, 2006).

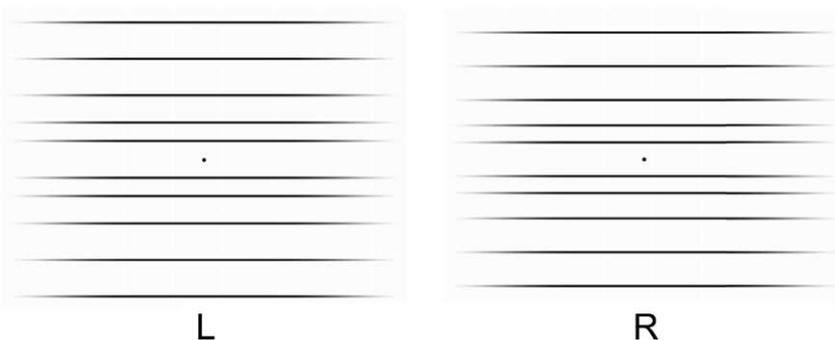


Fig. 2. Adaptation stimulus. The stimulus contained a VSR signal, but no horizontal disparities. To prevent retinal afterimages, observers were instructed to fixate the central dot, which moved up and down sinusoidally at 1 Hz.

using a display similar to Fig. 1, in which the VSR was 1, by asking observers to adjust the horizontal gradient of horizontal disparity (equivalently, horizontal size ratio or HSR) of a dot row to make the dot row appear unslanted.

Our initial question was whether there was adaptation to VSR. After finding an adaptation aftereffect, we asked whether adaptation occurred within a mechanism that measures VSR; and if not, what might account for it. Our results support the following conclusions. There is adaptation to VSR, adaptation does not occur within a mechanism that measures VSR, and VSR is used to rapidly recalibrate the use of EP signals for purposes of stereoscopic slant perception.

## 2. General methods

Data were collected at both York University (Experiments 1 and 3), and the University of Pennsylvania (Experiments 1, 2, and 3). There were no substantial differences between the data collected at York and Penn, so data were combined when computing group means.

### 2.1. Adaptation stimuli

We measured the slant aftereffect using a slant-nulling task. Thus, to test for adaptation to vertical disparity per se, without confounding effects of adaptation to the apparent slant of the surface, we needed an adaptation stimulus whose VSR could be defined by the experimenter, but always appeared unslanted (e.g., Berends & Erkelens, 2001; Duke & Wilcox, 2003; see also Domini, Adams, & Banks, 2001). To test for adaptation to VSR alone, we needed an adaptation stimulus that frustrated the measurement of HSR by the visual system. Both of these desiderata were achieved by using a stimulus that consisted of horizontal lines with gradually fading ends (so the endpoints could not be easily localized), as shown in Fig. 2. The lines were located at  $\pm 2^\circ$ ,  $4^\circ$ ,  $7^\circ$ ,  $10.5^\circ$ , and  $15^\circ$  of vertical separation from the centre of the image, and were approximately  $40^\circ$  wide. The lines were faded over approximately  $9^\circ$  at each end. Changing the HSR in this display did not cause the lines to appear slanted, but when these unbroken horizontal lines were changed to dashed lines, changing HSR

produced clear slant (though possibly less than veridical due to conflicting perspective and accommodation cues that signaled zero slant, see Gillam & Ryan, 1992). We can therefore conclude that the measurement of HSR was indeed frustrated in our horizontal line stimuli. Lines were positioned vertically to within 0.1 mm on the screen, using a spatial calibration and antialiasing procedure (Backus et al., 1999) so that VSR was specified with an estimated error of less than 0.007 by the lines at  $\pm 2^\circ$  (precision was greater for the more eccentric lines because constant error in position translates to greater precision in the specification of VSR as line separation increases).

Images were created by first computing the images that would be created at the left and right eyes by real lines in space on an unslanted surface 45 cm directly in front of the observer. Then, the vertical disparities were manipulated by vertically magnifying one image and vertically minifying the other. For example, a nominal VSR of 1.08 was achieved by 4% vertical magnification ( $\times 1.04$ ) in the left eye and 4% vertical minification ( $\div 1.04$ ) in the right eye to give a actual VSR of 1.0816.

The resulting pattern of vertical disparities approximates that produced by a gaze-normal surface in eccentric gaze; the gaze angle ( $\gamma$ , in radians) that corresponds to a given value of VSR is

$$\gamma \approx \frac{d}{I} \ln \text{VSR} \quad (1)$$

where  $I$  is the interocular distance and  $d$  is the distance to the fixation point. Note that positive gaze angles represent left gaze. (The natural log is used not for any theoretical reason, but for convenience because  $\ln(1 + \varepsilon) \approx \varepsilon$  for small  $\varepsilon$ .)

Vertical magnification did not change the apparent slant of the surface in the adaptation stimulus, nor its apparent head-centric direction. It remained apparently unslanted,<sup>3</sup> in forward gaze. Fig. 1 and Experiment 3 verify that the

<sup>3</sup> That the lines remained apparently unslanted is interesting in its own right. It implies that horizontal disparities are *necessary* for the construction of stereoscopic depth percepts, and that vertical disparities play only a modulating role, consistent with theory (Backus et al., 1999). In principle, in the absence of an HSR signal, the visual system might assume a default value of HSR = 1; this appears not to be the case.

vertical disparities in these stimuli were measured by the visual system, but they evidently had perceptual effects only in the presence of horizontal disparities.

During adaptation, vergence was maintained by fixating a single, central dot which oscillated sinusoidally in the vertical direction (through  $1.5^\circ$  at 1 Hz). This was done to prevent the formation of afterimages of the lines (Blakemore & Sutton, 1969).

## 2.2. Test stimuli and task

We used two types of test stimulus (“H” and “HV” test stimuli, respectively; Fig. 3) to measure the effects of adaptation to the above stimuli. Both contained a centered horizontal row of 23 stereoscopic dots, approximately  $22^\circ$  in width. To prevent the wallpaper illusion, the positions of all but the central dot were jittered in the vertical and horizontal directions (before projection to each eye’s image) by a small, randomly chosen amount (between  $-0.2^\circ$  and  $0.2^\circ$ ). The slant of this row about a vertical axis could be adjusted by the observer, by varying its HSR. The task was to set the slant of the dots to be gaze-normal, i.e., a slant nulling task. Aftereffects were measured as the difference between post- and pre-adaptation settings.

The H test stimulus contained an HSR signal but no VSR signal. At York University, the H test stimulus for both eyes contained only the dot row, and at the University of Pennsylvania, it contained only the dot row for the left eye, and both the dot row and horizontal lines like those in the adaptation stimulus for the right eye (so its cyclopean appearance was similar to the HV test stimulus described below). At York, for the H test stimulus, both eyes were shown an image like that of Fig. 3A; at Penn, the left eye was shown an image like Fig. 3A and the right eye was shown an image like Fig. 3B.

The HV test stimulus contained both HSR and VSR signals. The horizontal lines, as shown in Fig. 3B, were visible to both eyes. In Experiments 1 and 2, the VSR in the HV

test stimulus was always equal to 1, and in Experiment 3 it varied from 1.08 to  $1/1.08$ .

As a result of construction, slant in the H test stimulus was stereoscopically visible only through the use of HSR–EP. However, slant in the HV test stimulus was visible through the use of both HSR–VSR, and HSR–EP. Thus if adaptation to VSR occurs at the level of a VSR-sensitive mechanism, we would expect an aftereffect in the HV condition, but no aftereffect in the H condition. On the other hand, if adaptation causes recalibration in the use of extraretinal gaze signals, then we would expect an aftereffect in the H condition, and perhaps also a diminished effect in the HV condition.

## 2.3. Apparatus

Computer generated stereoscopic images were displayed on a pair of CRT monitors, viewed in a mirror stereoscope. The images were spatially calibrated and luminance was linearized using a photometer to estimate the video gamma function, which allowed accurate subpixel positioning of the stimuli. The viewing distance to the monitors was 45 cm. At York, a tightly fitting head and chin rest minimized movements of the observer’s head, and a pair of occluders either side of the head restricted the field of view only to the stereoscopic images. At Penn, a bite bar restricted head movements. In Experiment 2, gaze angle was made to vary between  $-16^\circ$  and  $+16^\circ$  by rotating the mirror ensemble  $\pm 8^\circ$  about a vertical axis that contained the observer’s cyclopean eye. A black jagged mask, made of cardboard that was cut with an approx. 3 cm triangle-wave serration, occluded the frame around one of the CRTs to prevent stereo matching of the two monitors’ borders that might otherwise have been possible using reflected light from the CRTs. All experiments were run in complete darkness and only the computer images were visible. Observers’ responses were made using a numeric keypad.

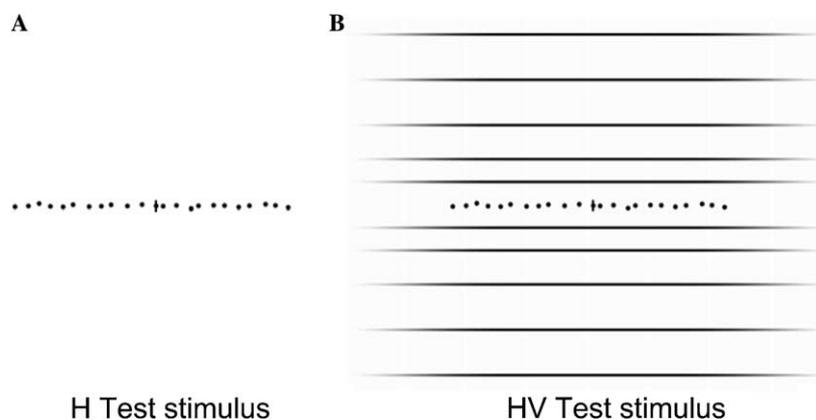


Fig. 3. Test stimuli, as they appeared when binocularly fused. The “H” test stimulus, left, consisted of a binocularly viewed horizontal dot row. It contained an HSR signal but no measurable VSR signal. The “HV” test stimulus, right, contained both HSR and VSR signals. At the University of Pennsylvania, the H test stimulus also contained monocularly visible horizontal lines; thus the appearance of the stimuli was similar in the H and HV conditions but it was still the case that only the HV test stimulus contained a VSR signal.

## 2.4. Procedure

Observers were given practice to familiarize themselves with the task. At the beginning of each trial, the test stimulus was assigned a randomly chosen HSR in the interval 1/1.05 to 1.05. During an experimental session, observers made 6 (York) or 8 (Penn) pre-adaptation settings of apparent gaze-normal, followed by a 2 min period of adaptation, followed by 6 or 8 post-adaptation settings. Of these settings, half were made with ‘H’ test stimuli and half were made with ‘HV’ test stimuli, with each type of setting being made alternately, and counterbalanced for order over two sessions. Thus there were 3 or 4 pre-adaptation settings and 3 or 4 post-adaptation settings for both H and HV test stimuli, in a given session. During adaptation (and the adaptation top-up periods) observers were instructed to track the oscillating fixation dot. There was no restriction on eye movements during settings. Each session lasted approximately 15–20 min.

To make a setting, the observer viewed the test stimulus for 1.5 s, followed by a bright mask (<0.1 s) to eliminate any monitor phosphor persistence and retinal afterimages. (The mask was a circle of approximately  $26^\circ$  in one image and a rectangle of approximately  $44^\circ \times 35^\circ$  in the other, alternated between trials; it contained no useful disparities.) In the case of post-adaptation settings only, each presentation of the stimulus was preceded by a “top-up” exposure to the adaptation stimulus, that lasted 10 s. The observer then pressed a key to indicate a desired change in the test stimulus, corresponding to one of six changes in HSR ( $\pm 0.018$ ,  $\pm 0.006$ , and  $\pm 0.002$ ). After as many presentations and adjustments as necessary, the observer indicated that he or she was satisfied with the setting, by pressing a separate key. To help stabilize their settings, observers were asked to “bracket” their responses by adjusting the dot row to appear slanted in both directions before indicating satisfaction.

## 3. Experiment 1: Adaptation to VSR

### 3.1. Methods

#### 3.1.1. Observers

Twelve volunteers between the ages of 20 and 40 participated in Experiment 1. Four were the authors, and the remaining eight were naïve to the hypotheses in the experiment. The naïve observers were paid. All observers had normal or corrected visual acuity, with stereoacuity of 30 arcsec or better. One observer from York and five observers from Penn were unable to perform a gaze-normal stereo adjustment task during a screening procedure, and did not participate. All testing was done under protocols approved by institutional review for human subjects.

#### 3.1.2. Procedure

All stimuli were presented in forward gaze. The adaptation stimulus contained one of five levels of VSR: 1/1.08, 1/

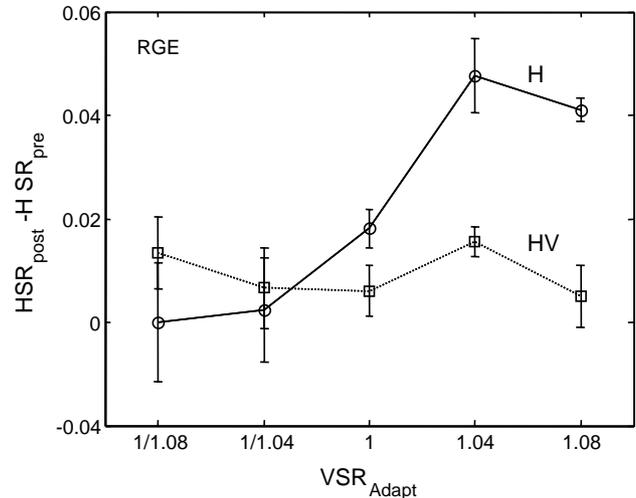


Fig. 4. Aftereffects for one observer in Experiment 1. The abscissa plots the VSR during adaptation and the ordinate plot the magnitude of the aftereffect, measured as a difference in the HSR settings that were seen to be gaze normal before and after adaptation. Data series are shown for the two conditions, H (in which the test stimulus contained no VSR signal), and HV (in which the test stimulus contained a VSR signal of 1).

1.04, 1, 1.04 or 1.08, which are the VSRs natural for gaze angles of approximately  $-31^\circ$ ,  $-16^\circ$ ,  $0^\circ$ ,  $16^\circ$ , and  $31^\circ$ , respectively, at a distance of 45 cm and interocular distance of 6.5 cm. Each observer performed five sessions with adaptation stimuli shown in that order, and then five more sessions with adaptation stimuli in the reverse order. Note that all stimuli were presented in forward gaze, i.e.,  $\gamma = 0^\circ$ , hence all adaptation stimuli other than  $VSR = 1$  contained an unnatural pairing of VSR and EP.

### 3.2. Results and discussion

Data for each observer consisted of three or four pre-adaptation settings and three or four post-adaptation settings of HSR, for each of the two conditions (H and HV).

Fig. 4 shows adaptation aftereffects (post-adaptation setting minus pre-adaptation setting) for one observer, with size of the adaptation effect plotted against the adaptation VSR value ( $VSR_{Adapt}$ ).<sup>4</sup> Fig. 5 plots data from the HV (left panel) and H test conditions (right panel) for all observers separately. The mean of each series has been shifted to align pre- and post-adaptation settings at  $VSR_{Adapt} = 1$  to more clearly show the similarity of their shapes. The effect was of different magnitude for different observers, but was remarkably consistent in one respect: for every observer,

<sup>4</sup> Error bars in this figure were computed as follows. Data from the two sessions were separately normalized by subtracting off the session mean, after which the pre-adaptation data were combined across the two sessions (giving 8 data points for each of H and HV) and the post-adaptation data were combined (same). The error bars are SEs estimated for the difference between post- and pre-adaptation means, computed as the root summed-squares of the separate SEs for the normalized post- and pre-adaptation data.

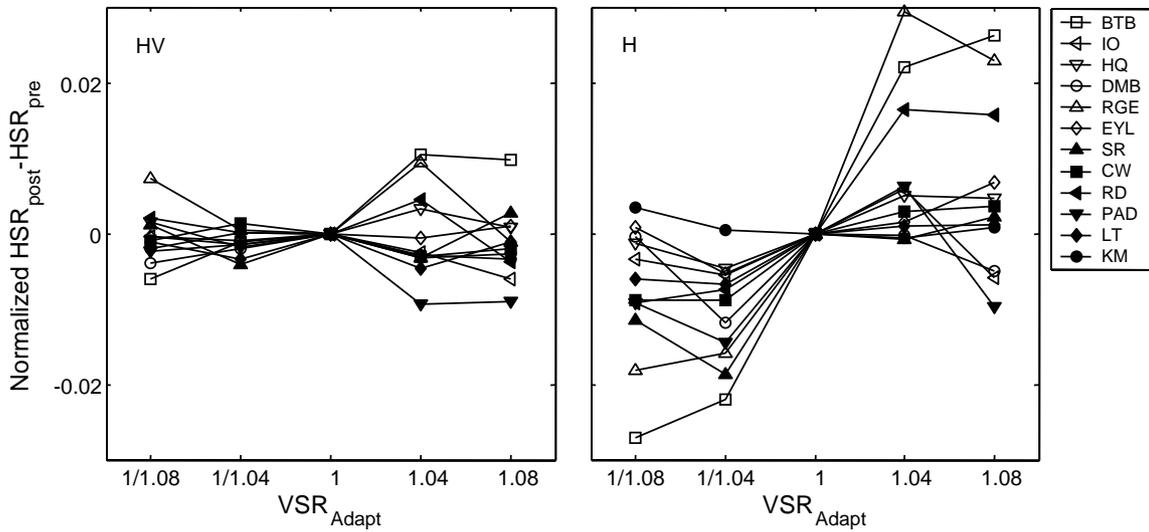


Fig. 5. Data from the 12 observers in Experiment 1. Adaptation aftereffects in the HV and H test conditions are shown in the left and right panels, respectively. Each observer’s data series has been normalized by subtracting off the aftereffect at adapting VSR = 1 to make the effects more visible.

the data had the same general shape, showing smaller effects in the HV condition than the H condition, and within the H condition, similar or even a reduced aftereffect for the two extreme values of adapting VSR (1/1.08 and 1.08) as compared to a linear prediction based on the moderate values (1/1.04 and 1.04). On average, the aftereffect did not increase further for adapting VSRs that deviated from 1 by more than 4%. Whilst there were individual differences, the aftereffects for the moderate adapting VSR values were significantly larger than those for the extreme values (one-tailed *t* test, *p* < .05).

Fig. 6 plots the magnitude of the aftereffect for the HV and H test stimuli, for each observer. The aftereffect is

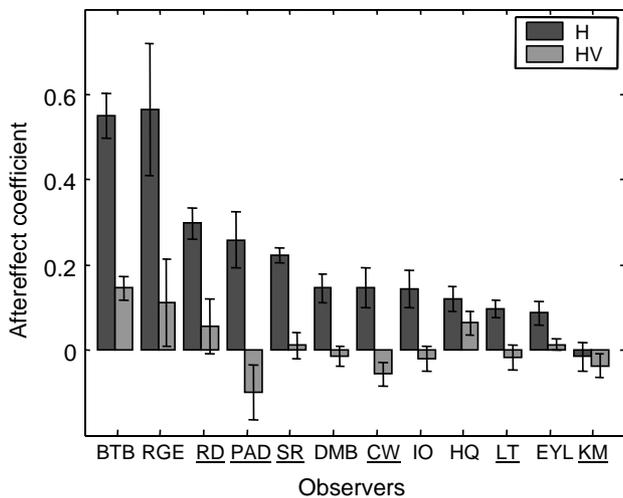


Fig. 6. Aftereffect coefficients for the 12 observers in Experiment 1, for the two test conditions (H and HV). The coefficient for each observer is computed as the slope of the line in the aftereffect graph that connects the data for VSR<sub>Adapt</sub> values of 1/1.04 and 1.04 (i.e., the difference in the two aftereffects, divided by 0.08). Error bars are root-summed-variance for the two settings at VSR<sub>Adapt</sub> values of 1/1.04 and 1.04, divided by 0.08. The underlined observers were tested at York University, and the others at University of Pennsylvania.

quantified by calculating the “aftereffect coefficient.” The coefficient for each observer is computed as the slope of the line in the aftereffect graph that connects the data for VSR<sub>Adapt</sub> values of 1/1.04 and 1.04 (i.e., the difference in the two aftereffects, divided by 0.08). This statistic gives the magnitude of the aftereffect as a proportion of the aftereffect that would be caused by complete adaptation. A coefficient of 0 indicates no adaptation and 1 indicates that adaptation induced a bias (in the HSR that appears gaze-normal) equal to what would be needed to indicate gaze-normal, according to theory for the HSR–VSR estimator, if the dot row were presented with the VSR of the adapting stimulus. This statistic is, ex hypothesi, the coefficient of recalibration.

The first important point from the graphs is that the HV test stimuli did not produce a repulsive aftereffect as predicted by our first hypothesis, which was that adaptation occurs in the measurement of VSR. A few observers exhibited small attractive aftereffects in the HV condition but most were close to zero and the group mean aftereffect coefficient was  $0.01 \pm 0.02$  (mean  $\pm$  SE). This result supports the conclusion that low-level VSR sensitive mechanisms do not adapt, and was surprising to us because adaptation is so pervasive in perception.

The second important point is that condition H produced systematic slant aftereffects of the same sign as VSR<sub>Adapt</sub>, i.e., attractive aftereffects. The group mean aftereffect coefficient for the H condition was  $0.22 \pm 0.05$ . Since the aftereffects are largest for the H stimuli, which do not contain a VSR signal, this effect cannot be due to adaptation in the mechanism that measures VSR. These attractive aftereffect data are, however, consistent with our second hypothesis: that adaptation to VSR causes recalibration in the use of EP for stereopsis. The smaller aftereffects observed in the HV condition for some observers (BTB, RGE, RD and HQ) is also consistent with this interpretation, if the slant percept for those test stimuli

was determined from the weighted combination of a recalibrated estimate based on HSR–EP, and an unchanged estimator based on HSR–VSR. Because the aftereffects in the H condition are in the same perceptual direction as would normally be caused by the VSR in the adaptation stimulus, the data might also be interpreted as a “perseveration” of the  $VSR_{Adapt}$  signal within the visual system, in which  $VSR_{Adapt}$  is used to interpret the HSR signal even after the VSR signal is no longer present in the stimulus. This latter explanation seems less likely to us for reasons we take up in Section 6.

The third point to note from the results is that aftereffect magnitudes in the H condition are not related to  $VSR_{Adapt}$  by a simple linear function, such as the 25% depth aftereffect often found in adaptation experiments (Howard & Rogers, 2002). Instead, we found the largest effects at intermediate values of  $VSR_{Adapt}$ . We will return to this feature of the data in the discussion of Experiment 3.

#### 4. Experiment 2: Adaptation to VSR in eccentric gaze

The results of Experiment 1 suggest that adaptation to conflicting VSR and EP signals causes recalibration of the EP signal in stereopsis. Here we examine this idea further. The hypothesis of recalibration in the use of EP makes an interesting prediction: adaptation aftereffects should be observed whenever  $VSR_{Adapt}$  is inconsistent with EP signals, so it should be possible to create aftereffects using a  $VSR_{Adapt}$  stimulus with a value of 1, if the adaptation stimulus is viewed in eccentric gaze. Also, the aftereffects we found in the H test condition of Experiment 1 for  $VSR_{Adapt}$  values of  $\pm 1.04$  should be reduced or eliminated, when the adaptation stimulus is viewed in left or right eccentric gaze, respectively. Finally, consistent with Experiment 1, HV test conditions should not produce repulsive aftereffects in any condition if adaptation does not occur at the level of VSR measurement. We tested these predictions in Experiment 2.

##### 4.1. Methods

###### 4.1.1. Observers

Seven volunteers between the ages of 20 and 40 participated in Experiment 2. Four were the authors and three were naïve to the hypotheses of the experiment. All observers had normal vision or vision corrected to normal by contact lenses.

###### 4.1.2. Procedure

The stimuli and experimental procedure were similar to Experiment 1, using adaptation stimuli with  $VSR_{Adapt}$  values of  $1/1.04$ , 1 and 1.04, which corresponded to gaze angles of  $-16^\circ$ ,  $0^\circ$ , and  $16^\circ$ . In the three *cue-consistent* conditions, these adaptation stimuli were presented at the corresponding gaze angle. Gaze angle was manipulated by rotating both haploscope mirrors by  $\pm 8^\circ$  about an axis of rotation that passed through the observer’s cyclopean

eye. The vergence angle was thereby kept constant, resulting in a vergence distance of 43.3 cm in eccentric gaze (fixation on the 45 cm Vieth–Müller circle). In the two *cue-conflict* conditions,  $VSR_{Adapt}$  was 1 (i.e., signalled  $0^\circ$  gaze) at gaze angles of  $\pm 16^\circ$ . Thus, there were five adaptation conditions, tested in separate experimental sessions. Each observer performed all 5 sessions first in one order, and then again, in the reverse order. Test stimuli were presented at the same gaze angle location as the adaptation stimulus and comprised both H and HV conditions. VSR was 1 in all of the HV test stimuli.

##### 4.2. Results and discussion

Data for each observer in Experiment 2 were four pre-adaptation settings and four post-adaptation settings of HSR, in each of the two test conditions (H and HV), for each of five adaptation conditions. Data from all the conditions are plotted for one observer in Fig. 7. Fig. 8 shows aftereffect coefficients for the four combinations of H and HV, vs. cue-consistent and cue-inconsistent, for each observer, calculated in the same manner as Experiment 1.

Considering each of the four types of condition in turn, the largest adaptation aftereffects were produced in the H test conditions from cue-conflict stimuli. This is true for the group data in Fig. 8, although not for all observers separately. Across observers, the aftereffect coefficient for H-inconsistent was  $0.17 \pm 0.08$  (mean  $\pm$  SE; significant at the  $p < .05$  level in a one-sided  $t$  test of difference from zero). The aftereffect magnitudes are variable between observers; this variability can be interpreted in a meaningful way as we describe later. The most important point is

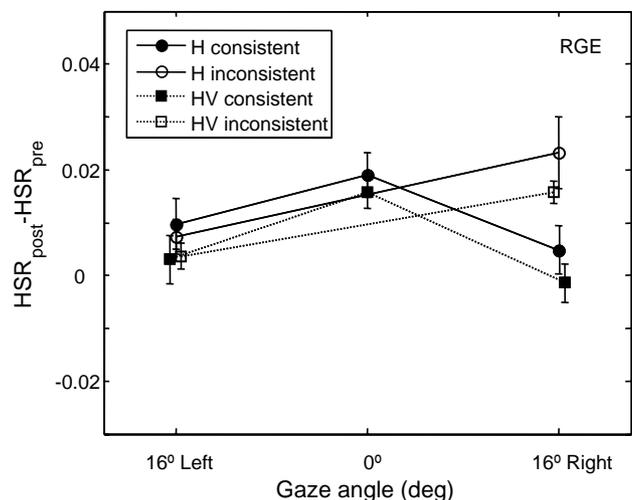


Fig. 7. Aftereffects for one observer in Experiment 2. The abscissa plots the eyes’ physical gaze angle relative to the head, and the ordinate plot the magnitude of the aftereffect. Data are shown for the four conditions, H consistent, H inconsistent, HV consistent, and HV inconsistent. Test stimuli in the H and HV conditions were as in Experiment 1. In the “consistent” conditions, the gaze angle was equal to what would naturally co-occur with the adapting VSR; in the “inconsistent” conditions, VSR was 1 for adaptation in eccentric gaze.

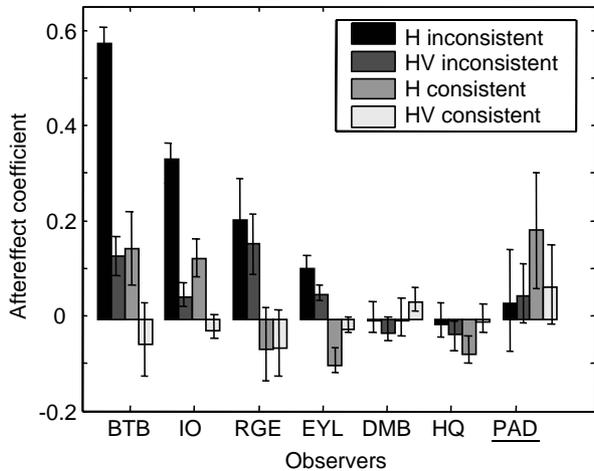


Fig. 8. Aftereffect coefficients for the seven observers in Experiment 2, for the four test conditions. The coefficient is the difference in aftereffects for the positive and negative eccentric gaze conditions, divided by 0.08 (i.e., divided by the difference in VSR that would normally occur across this change of eccentricity). The data have been offset slightly in the horizontal direction to make them more visible.

that the aftereffects are in the predicted direction if the use of EP was recalibrated by exposure to a conflicting VSR.

Second, aftereffects for the H test stimulus after cue-consistent adaptation (“H-consistent” conditions) were for the most part small compared to aftereffects after cue-inconsistent adaptation. This is evident from the observer data (third bar in each group) in Fig. 8. Across observers, the aftereffect coefficient in the H-consistent conditions was  $0.03 \pm 0.04$  (not significantly different from zero). The eye position recalibration hypothesis predicts zero aftereffects in these conditions. A small same-sign aftereffect could have been caused in some observers by EP adaptation due to maintaining eccentric gaze for a prolonged period.

Third, HV test stimuli produced aftereffects close to zero in both the inconsistent and consistent conditions. The aftereffect coefficients were  $0.05 \pm 0.03$  ( $p < .05$ , one-tailed) and  $0.01 \pm 0.02$  (not significant). The former replicates the finding from Experiment 1 that VSR measurement itself did not adapt. The latter is consistent with the recalibration hypothesis, because recalibration in the use of EP should occur only in case of a conflict between EP and VSR.

As noted above, the H test stimuli in the cue-inconsistent condition produced widely varying aftereffect magnitudes across observers: the range of coefficients was from  $-0.01$  to  $0.55$ . The eye position recalibration hypothesis predicts the largest aftereffects in this condition, so on the face of it, the finding of relatively weak aftereffects for some observers is unresponsive of this hypothesis. However, we suggest an alternative explanation. Aftereffects mediated by EP signals will depend on the extent to which EP signals are used in slant perception; observers who make little use of EP might be expected not to recalibrate its use. The extent to which observers made use of the EP signal for purposes of estimating slant from HSR can be determined in this experiment from the pre-adaptation settings of HSR

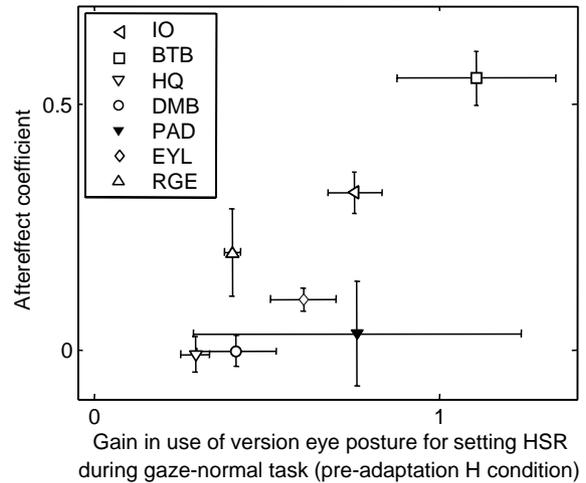


Fig. 9. Aftereffect coefficient as function of reliance on eye posture, across observers, in Experiment 2. The abscissa is an index of the extent to which the observers’ HSR settings depended on gaze angle for H test stimuli, measured during pre-adaptation trials. The data show that across observers, reliance on gaze angle to see slant was positively correlated with the adaptation aftereffect ( $r = 0.80$ ,  $p = .03$ ).

in the H test stimulus. Fig. 9 shows that change in null settings for HSR, across changes in gaze angle, was positively correlated with the magnitude of the aftereffect. This is consistent with recalibration in the use of EP.<sup>5</sup>

Of the eight observers who participated in both Experiments 1 and 2, four (RGE, DMB, PAD, and HQ) had distinctly lower aftereffect coefficients in Experiment 2. Some decrease might be expected: the effective conflict between VSR and EP was probably smaller in this experiment because the conflict was created using  $VSR = 1$  in eccentric gaze, and gaze angle tends to be underestimated for purposes of correcting horizontal disparity. For example, Backus et al. (1999) found that HSR was undercorrected when slant estimates were based only on HSR and EP.

### 5. Experiment 3: Induced effect

The results of Experiments 1 and 2 provided no evidence to suggest the mechanism that measures VSR is susceptible to adaptation aftereffects. Instead, the results support the conclusion that EP signals are recalibrated by VSR signals when the two are in conflict. The degree of conflict alone, however, cannot explain the systematic pattern of aftereffects found in Experiment 1 since they were not linearly related to adapting VSR magnitude. The largest aftereffects were produced by adaptation to  $VSR = 1/1.04$  and  $1.04$ ,

<sup>5</sup> It is possible that HSR settings in pre-adaptation trials of the H test stimuli were influenced by the VSR value of 1 in the HV test stimuli, with which they alternated. Fig. 12 shows that relatively short exposures to VSR can affect settings in the H test stimulus; such an influence would cause HSR settings to be closer to the VSR value of 1, causing us to underestimate the true size of any adaptation aftereffects in the H test stimuli.

not 1/1.08 and 1.08. In the context of our recalibration hypothesis, this roll-off means that the visual system recalibrated its use of EP less in response to a large conflict than a small one. There are two possible explanations. First, it is already known that VSR is given less weight at high values (Ogle, 1938), and that this is the consequence of a robust estimation process (Landy, Maloney, Johnston, & Young, 1995) that downweights the use of VSR when the VSR-based slant estimate conflicts with estimates of zero slant based on EP and nonstereo cues (Banks & Backus, 1998). Thus, the conflict between the EP-based estimate of slant and the system's overall estimate of slant may have been smaller at the high VSR values. One would not expect the system to recalibrate EP to make it more like VSR, when conditions are such that it does not trust the VSR-based estimate.

Alternatively, the recalibration process might itself be robust, beyond what it inherits from cue combination. In other words, the system might trust small discrepancies more than large ones, for purposes of recalibration. In Experiment 3 we examine whether the roll-off of the aftereffect in Experiment 1 can be attributed entirely to the mechanism that combines slant estimates, or alternatively, whether some of it should be attributed to the mechanism that uses VSR to calibrate EP. If robust use of VSR in slant perception is responsible, then the effect of VSR on slant judgment (i.e., observer's induced effects) should be linearly related to their aftereffects in Experiment 1. Alternatively, a non-linear relationship would imply additional robustness in the calibration itself. Accordingly, we measured observers' induced effects in this experiment.

## 5.1. Methods

### 5.1.1. Observers and procedure

Participants were the same 12 observers who took part in Experiment 1, and the same slant-nulling method was used to measure the effect of VSR. There was a single test phase and no adaptation period. Test stimuli were viewed in forward gaze and comprised a central dot row with flanking horizontal lines as shown in Fig. 1, with VSR values of 1/1.08, 1/1.04, 1, 1.04, and 1.08 as in Experiment 1. Observers made 6 (or 8) apparent gaze-normal settings for each of the 5 test stimuli, which were presented in a random order.

### 5.2. Results and discussion

Data from Experiment 3 are shown in Fig. 10. For the range of VSR values (1/1.08 to 1.08) that we tested, the induced-effect was almost linearly related to VSR ( $r$  squared  $\geq 0.95$  for 10 of the 12 observers;  $r$  squared = 0.00 for RGE and 0.90 for BTB). The near-linear form of these data is clearly different from the rise-and-fall (or "roll-over") pattern of aftereffects found in Experiment 1. We therefore conclude that the reduced effectiveness of adaptation to VSR at values beyond 1/1.04 and 1.04 was not

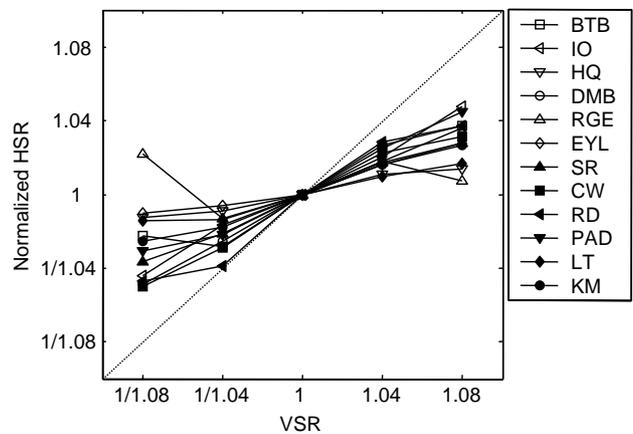


Fig. 10. Induced effect data from each observer in Experiment 3. The induced effect was attenuated less at large VSR values than were adaptation aftereffects at large adapting VSR values.

inherited from cue combination processes. The results of Experiments 1 and 3 together suggest that the visual system uses VSR to different extents for slant perception and for calibration of EP signals, and that EP calibration is a robust process.

Whilst VSR may be used to different extents in the two processes, it is possible that the same VSR representation is used in both. If so, observers' aftereffect coefficients should be positively correlated with their induced effect coefficients. Fig. 11 plots adaptation aftereffect coefficients measured in Experiment 1 against induced effect coefficients measured in Experiment 3, for 12 observers. The data are suggestive of a link between these two phenomena, but the correlation between the measures is not significant at the .05 level unless observer RGE, who showed the largest adaptation aftereffect of all, is excluded from the analysis. Whilst both effects obviously depend on the visual system's ability to measure VSR, there was no strong evidence that a common representation of VSR within the system determined the size of both effects.

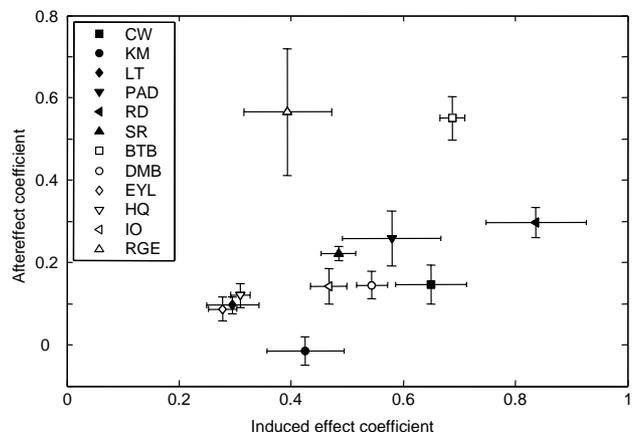


Fig. 11. Scatterplot of aftereffect vs. induced effect coefficients for 12 observers. Error bars are SEs. The data fail to show a reliable correlation ( $r = 0.40$ ,  $p = .2$ ).

## 6. General discussion

### 6.1. Recalibration in use of EP vs. perseveration of VSR

We have discovered an adaptation aftereffect to pure VSR signals. Contrary to expectation, it was not a repulsive (negative) aftereffect, but instead it was an attractive (positive) one. Furthermore, the aftereffect was much stronger for test stimuli that did not contain a VSR signal, than it was for stimuli that contain a VSR signal at the normative value of 1.0. What might cause this pattern of results? There are two possibilities: (1) the VSR value to which the observer was exposed during adaptation “perseverates,” i.e., remains in the system until the observer is exposed to a new VSR value. In this case, the adaptation value of VSR can be thought of as establishing a “VSR environment” within which HSR is interpreted as slant, even after the original VSR signal is removed from the display. (2) Exposure to VSR, even in the absence of HSR or perceived slant, causes adaptation in a mechanism that does not itself require VSR to produce a percept of slant.

We believe the second possibility better explains our data. There is indeed a mechanism that might, in principle, be recalibrated as a consequence of exposure to VSR: namely, the mechanism that uses EP (instead of VSR) to interpret HSR as slant. In our H test condition, recalibration in this mechanism could have produced data similar to perseveration of VSR.

There are also several reasons to believe that perseveration is unlikely. First, the visual system responds to changes in VSR at least as quickly as it responds to changes in HSR (Allison, Howard, Rogers, & Bridge, 1998; van Ee & Erkelens, 1998). There is no inherent lag in updating the internal representation of VSR when it changes, and thus, we surmise, no reason to suppose the system is unaware of the disappearance of VSR when it disappears.

Second, we know from previous studies that when the visual system has both methods of estimation available to

it—HSR–VSR, and HSR–EP—the weights accorded the two estimates reflect their actual reliabilities. The weights are quantitatively predicted from the reliability with which the visual system can measure the signals needed to compute the estimate on a given trial (Backus & Banks, 1999). Therefore, we expect the system to give no weight to an estimate based on HSR–VSR in the H test stimulus, and identify the mechanism that estimates slant from HSR–EP as a candidate locus for the adaptation effect.

Third, a simple model of perseveration is that the most recently measured VSR value persists until it is replaced. Unlike recalibration in a different mechanism, this predicts no effect of adaptation duration on the magnitude of the aftereffect. Fig. 12 shows data for a control experiment, run on the two observers who showed the largest adaptation aftereffects. In this experiment, unlike Experiment 1, there was no initial 2-min adaptation period. The adapting stimulus was shown before each viewing of the stimulus, in the same manner as the top-up stimuli of Experiment 1, but this time the top-up stimulus had one of three durations (tested in different blocks): 10 s (as in Experiment 1), 3, or 1 s. Critically, VSR during the top-up period was reversed from one trial to the next. In other words, the same VSR was presented before each keypress during a given adjustment, but after the test stimulus was accepted as gaze-normal, the reciprocal VSR was used during top-ups for the next setting. A small aftereffect resulted even from a mere 1 s exposure to VSR, but the magnitude of the aftereffect increased to several times this value as the duration of exposure to the adaptation stimulus was increased. A simple version of the perseveration hypothesis does not account for these data; one has to suppose greater perseveration of VSR for longer exposure durations.

Finally, recall that observers in Experiment 2 who relied more on HSR–EP to estimate slant showed the greatest adaptation aftereffects; this is consistent with the notion that adaptation caused recalibration in that mechanism. In short, although we cannot completely rule out

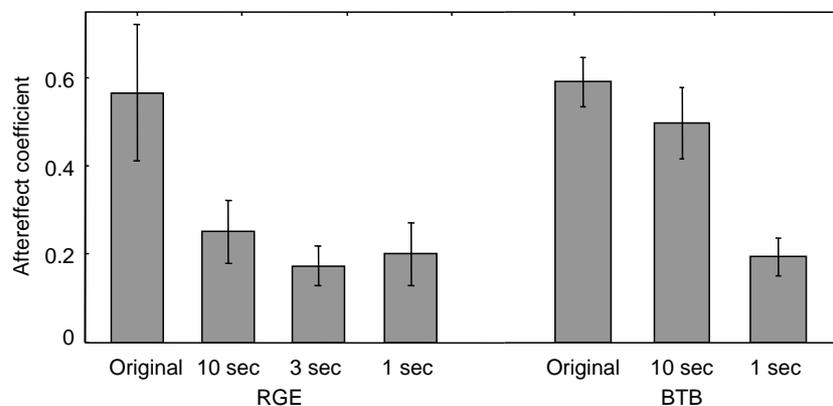


Fig. 12. Effect of adaptation duration for the two observers with the largest aftereffects. The bar labeled “Original” shows data from Experiment 1. The other bars show data collected without a long (90 s) adaptation period, using adapting VSRs that alternated in signum log (i.e., greater than 1, less than 1, ...) from trial to trial. The duration of exposure to the adapting VSR stimulus before each setting was its nominal “top-up” duration (10, 3, or 1 s) as labeled in the figure.

perseveration of the VSR signal as a component in the aftereffect, we are quite sure that perseveration does not account for all of it.

### 6.2. Recalibration in the use of eye position for estimating slant

The most obvious reason for the system to recalibrate the HSR–EP mechanism is if the slant estimate it produced were to disagree with the estimate produced by HSR–VSR. This discrepancy might serve as an error signal to stimulate recalibration (Wallach, 1968). However, there is no way to estimate slant from either HSR–VSR or HSR–EP in our VSR adaptation stimulus. Thus, the cause for recalibration must be discrepancy between EP and VSR. These two signals are normally highly correlated at any given viewing distance. Thus it is plausible the system could detect a systematic mismatch between these signals, relative to previous experience, and respond by recalibrating one or both signals, or the slant estimator(s) that use the signals.

Two models for such a recalibration are shown in Fig. 13. Both can explain our results. The left model embodies a standard “weak fusion” cue combination scheme (Clark & Yuille, 1990; Landy et al., 1995), up to the computation of separate estimates for slant (these are later combined into a single estimate; see Backus et al., 1999). To explain the adaptation aftereffects in this model, we suppose that the system can detect discrepancies in VSR and EP, and adjust one signal or the other, or both, before use for slant perception. Empirically, we observe that adaptation causes a change in the use of the EP signal, not the VSR signal; the reason for this is probably that the internal EP signal is more likely than the VSR signal to develop systematic bias; if the system knows this to be the case (e.g., by monitoring cue stability), it would sensibly recalibrate the EP signal, to accord with the VSR signal, rather than vice versa (Backus, 2003; Bradshaw, Glennerster, & Rogers, 1996). Note that no stereoscopic slant estimate is needed for recalibration; in this model, recalibration can occur in

the absence of the HSR signal, as would be required to explain adaptation aftereffects in our experiments.

The right model in Fig. 13 embodies a “strong fusion” scheme, in which a single function takes as its input all of the signals, and delivers its best estimate of slant. Its operation is akin to multidimensional table look-up. This model implements a general, Bayesian estimation: perceived slant is modeled as the slant in the world most likely to have caused the observed set of input-signal measurements. In the case of our adaptation stimulus, *no slant is likely to have caused the observed signal measurements*, and we suppose that this condition causes adjustment of the lookup table; we are forced to suppose that this component of the estimator mechanism is capable of recalibrating itself independently, in the absence of HSR input. Again, we suppose the function adjusts itself according to a rule that takes into account which of the various input signals is most likely to be corrupted by systematic bias (i.e., has lower stability).<sup>6</sup> The table must be adjusted in the absence of HSR, in such a manner that a slant estimate based on HSR–EP alone will reflect the recalibration, even after the VSR signal has been removed.

### 6.3. Use of extraretinal eye position signal for estimating slant vs. visual direction

Neither Banks, Backus, and Banks (2002) nor Berends, van Ee, and Erkelens (2002) found an instantaneous effect of VSR on perceived visual direction (relative to the observer’s trunk). This is probably because EP is more reliable than VSR for estimating headcentric direction (Backus et al., 1999). However, Berends et al. (2002) reported a small change in apparent straight-ahead, in 5 of 9 observers, after 5 min of adaptation to stimuli that contained a conflict between VSR and EP, consistent with recalibration of EP. The test stimulus in those experiments contained not only a small probe but also a large surround, so any bias to assume stationarity of the surround would have reduced the measured effect size. The visual system could recalibrate its use of a given signal at the site where the signal is measured, in which case all systems that use the signal would be affected, or it could recalibrate a single mechanism that uses the signal, in which case only that mechanism would be affected (or some recalibration could occur at both sites). Additional experiments using test stimuli without a visual surround could in principle tease these components of adaptation apart.

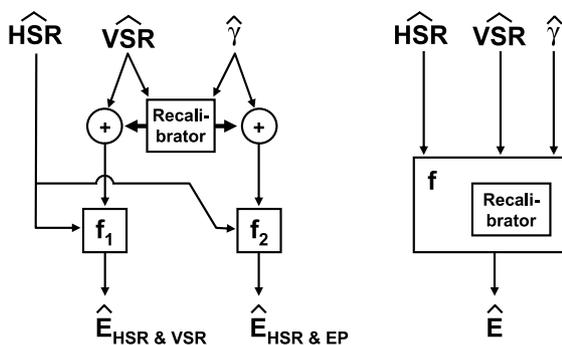


Fig. 13. Two hypothetical mechanisms to recalibrate use of an extraretinal gaze angle signal during stereoscopic slant perception. Left: recalibration occurs before use of the signal to calculate slant in  $f_2$ , an estimator that uses HSR and eye position. Right: recalibration is inherent in the function that calculates slant, shown here as a single function (strong fusion model).

<sup>6</sup> To be more precise: suppose VSR and EP are compared according to their equivalent azimuths. The system’s best estimate of azimuth is given using cue weights that are proportional to reliability; both estimators should move towards this value (Ghahramani, Wolpert, & Jordan, 1996) but we would expect the rate of movement to reflect not only difference between the estimate and system’s best estimate, but also knowledge about stability. The extreme example of a low-reliability, high-stability estimator is a Bayesian prior (Backus, 2003).

#### 6.4. Adaptation to the induced effect

Several studies have examined the effect of prolonged exposure to a relative vertical magnification between the two eyes' images (e.g., Lee & Ciuffreda, 1983; Miles, 1948; Morrison, 1972). In these studies, subjects wore meridional lenses which introduced an overall vertical-size disparity during otherwise natural viewing. Apparent slant, i.e. the induced effect, was introduced into surfaces in the scene as a consequence of wearing the lenses, and this diminished over time. Lee and Ciuffreda (1983) used an apparently frontal plane setting task, in which both HSR and VSR signals were available, and took measurements periodically over 4 h. They found that a 4% vertical magnification initially produced between 40 and 85% of the predicted initial induced effect, which diminished to 20–45% in less than an hour. The stimulus for adaptation in this case is quite complicated, as adaptation may involve VSR, HSR, EP, pictorial depth cues and perceived slant. They accounted for their results in terms of recalibration of the relationship between VSR and apparent slant due to the conflict of VSR with both HSR and pictorial depth cues. In this account, VSR signals are recalibrated to agree with HSR and pictorial cues. The effect that we observed cannot be explained in the same way because our H test stimuli provided no VSR information. Our results can be accounted for by the use of VSR to recalibrate EP. It is possible that EP signal recalibration also occurred in previous studies, but it cannot explain the diminishing induced effects because the effect is in the opposite direction.

Data consistent with recalibration of EP were reported by Berends and Erkelens (2001). Their adapting stimuli contained horizontal and vertical disparities that were adjusted to make the surface appear unslanted. After 5 min adaptation, a test stimulus was shown that contained good horizontal disparity information but poor vertical disparity information (it had small vertical size). Significant, systematic aftereffects were measured and the authors suggested the cause was either adaptation to horizontal disparity or recalibration of EP. We have now observed similar effects after adaptation to stimuli that do not contain horizontal disparities, so we can rule out the possibility that horizontal disparity adaptation accounts for all of the effect they observed.

#### 6.5. Adaptation to stereoscopic depth: Implications for disparity processing

When an object slanted in depth is viewed for a prolonged period, its apparent slant diminishes as discussed above, and the apparent slant of subsequently viewed objects is similarly biased. Kohler and Emery (1947) found that inspection of a slanted line causes a frontal test line to appear slanted in the opposite direction and to a lesser degree. It has been shown that purely binocular depth aftereffects can be produced by adaptation to depth depicted in random dot stereograms (Blakemore & Julesz, 1971; Long & Over, 1973).

Theories of binocular depth aftereffects typically propose a role of adaptive horizontal disparity tuned channels (see Howard & Rogers, 2002). Such accounts are attractive given the success of the tuned channels approach in explaining other aftereffect phenomena (e.g., aftereffects of tilt, spatial frequency and motion), for which there is support from both physiological and psychophysical studies (Blakemore & Campbell, 1969; Campbell & Kulikowski, 1966; Gibson & Radner, 1937; Gilinsky, 1968; Hammond, Mouat, & Smith, 1985; Hubel & Wiesel, 1962; Pantle & Sekuler, 1968; Thompson, 1998; Huk, Ress, & Heeger, 2001). Furthermore, there is a wealth of both psychophysical and physiological evidence for the existence of disparity tuned channels (e.g., Hubel & Wiesel, 1970; Julesz & Miller, 1975; Poggio, Gonzalez, & Krause, 1988; Yang & Blake, 1991), so it is perhaps surprising that an adaptation aftereffect attributed to such mechanisms has not been confirmed.

Domini et al. (2001) found that adaptation to different combinations of horizontal disparity and vergence produced aftereffects of depth curvature that varied with the simulated depth curvature of the adaptation stimuli, rather than their horizontal disparities. Hence an adaptive disparity sensitive mechanism was not revealed. Instead, their result indicated an adaptive mechanism sensitive to 3D shape. Such a 'high-level' mechanism was also suggested by the results of Balch, Milewski, and Yonas (1977), who found that adaptation to depth from disparity or pictorial cues produced a depth aftereffect with test stimuli defined by either cue.

Duke and Wilcox (2003) showed that depth aftereffects produced by adaptation to stimuli in which apparent depth is produced by *horizontal* disparity modulations are the same as those produced by stimuli with the same apparent depth induced by *vertical* disparity modulations. Whilst this result is consistent with adaptation to apparent depth, these depth aftereffects could be explained instead by adaptation of a horizontal disparity sensitive mechanism in the first case, and a vertical disparity sensitive mechanism in the second. However, in the present study we found no evidence of adaptation in a mechanism that measures vertical disparities. This result therefore argues against disparity adaptation as an explanation of the depth aftereffects of Duke and Wilcox (2003), and thus, of other conventional stereoscopic depth aftereffects.

Berends, Liu, and Schor (2005) recently tested whether horizontal disparity (HSR) adaptation is responsible for slant aftereffects by measuring slant aftereffects at a number of different test distances after adaptation to a slanted surface at a fixed distance. They reasoned that if disparity adaptation causes the aftereffect, the magnitude expressed as disparity should be constant over the test distances. This was not found. Instead, the aftereffects at different distances were more similar when expressed as degrees of slant, consistent with adaptation at the level of slant representation. From these various studies, we can conclude that neither horizontal nor vertical disparity gradients are

measured by a mechanism that adapts at seconds-to-minutes timescales.

#### 6.6. The visual system measures VSR separately from HSR

Matthews, Meng, Xu, and Qian (2003) recently argued that the induced effect can be understood as a confusion between horizontal and vertical disparity by the mechanisms that measure horizontal disparity (Arditi, Kaufman, & Movshon, 1981; Arditi, Kaufman, & Movshon, 1983; cf. Mayhew & Frisby, 1982). Truly, this view must be abandoned. First, VSR varies as a function of both azimuth and distance from the head; only by taking this into account can one accurately predict the complicated relationship between viewing distance and the strength of the induced effect (Backus & Banks, 1999). Second, VSR is a useful signal for the system to measure and there is no reason to think that measuring it would be difficult. Third, Kaneko and Howard (1997) showed that VSR is measured with different spatial resolution than HSR. Fourth, our HV test stimulus demonstrates directly that VSR and HSR both have effects on the perceived slant of a horizontal dot row, even though the signals are carried by different elements of the display that must be measured by different disparity detectors. Fifth, in the HV test stimulus the horizontal lines remained perceptually unslanted at all times; only the dot row was seen to rotate in depth. This is easily explained if VSR is measured regionally, but not if vertical and horizontal disparities are confused, since *only* the horizontal lines have vertical disparity, but *only* the horizontal dot row responds perceptually to that disparity. It also implies that horizontal disparities are *necessary* to the stereoscopic perception of slant.

#### 7. Conclusions

Aftereffects in a stereoscopic slant-nulling task were obtained after adaptation to a pattern of horizontal lines, in which vertical disparity signaled a particular vertical size ratio. The pattern did not contain horizontal disparities, and it looked frontoparallel. The aftereffect was in a positive direction, and its magnitude was larger for test stimuli consisting of a horizontal row of dots and therefore did *not* contain a VSR signal, than in test stimuli that contained both a horizontal row of dots and horizontal lines. Aftereffects were obtained even when the adaptation stimulus contained a VSR of 1, provided the gaze angle was eccentric (so that VSR and version were in conflict). This pattern of results could occur if the adapting stimulus effected a recalibration of the mechanism that computes slant using the version eye posture signal. When VSR can be measured, observers rely on it to null stereoscopic slant, because it is more reliable than using felt eye position (Backus & Banks, 1999). Thus, it is reasonable that the visual system would recalibrate its use of eye position when the two signals are inconsistent.

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