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**Supplementary information** is available on *Nature*'s World-Wide Web site (http://www.nature.com) or as paper copy from the London editorial office of *Nature*.

**Acknowledgements**

We thank J. Baker, J. Bale, J. Buonaccorsi, C. Frampton and R. Kinnersley for comments on the manuscript, and the University of Birmingham for funding assistance.

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# Distance determined by the angular declination below the horizon

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**A biological system is often more efficient when it takes advantage of the regularities in its environment[1,2]. Like other terrestrial creatures, our spatial sense relies on the regularities associated with the ground surface[2–6]. A simple, but important, ecological fact is that the field of view of the ground surface extends upwards from near (feet) to infinity (horizon)[2]. It forms the basis of a trigonometric relationship wherein the further an object on the ground is, the higher in the field of view it looks, with an object at infinity being seen at the horizon. Here, we provide support for the hypothesis that the visual system uses the angular declination below the horizon for distance judgement. Using a visually directed action task[7–10], we found that when the angular declination was increased by binocularly viewing through base-up prisms, the observer underestimated distance. After adapting to the same prisms, however, the observer overestimated distance on prism removal. Most significantly, we show that the distance overestimation as an after-effect of prism adaptation was due to a lowered perceived eye level, which reduced the object's angular declination below the horizon.**

Figure 1a illustrates the relationship between the angular declination below the horizon ($\alpha$) and the absolute distance ($d$) of an object on the ground from the observer. Assuming that the observer's eye height ($h$) is known[11], the object distance can be determined by obtaining the angular declination below the horizon: $d = h/\tan(\alpha)$ (refs 2–4). To test this 'angular declination hypothesis', that the visual system can access the information regarding the angular declination below the horizon for distance perception, consider the consequence of viewing through a pair of base-up prisms that deviate light by $\delta$ degrees (Fig. 1b). Predictably, the angular declination below the horizon will increase to $\alpha + \delta$, and, accordingly, the perceived distance, $h/\tan(\alpha + \delta)$, will decrease. Next, suppose that the observer continually views the visual environment through the base-up prisms, and eventually removes the prisms to reveal the after-effect of prism adaptation[12–14]. If we assume that prism adaptation induces a recalibration of the eye level downward, the angular declination below the horizon will also reduce. Thus, we

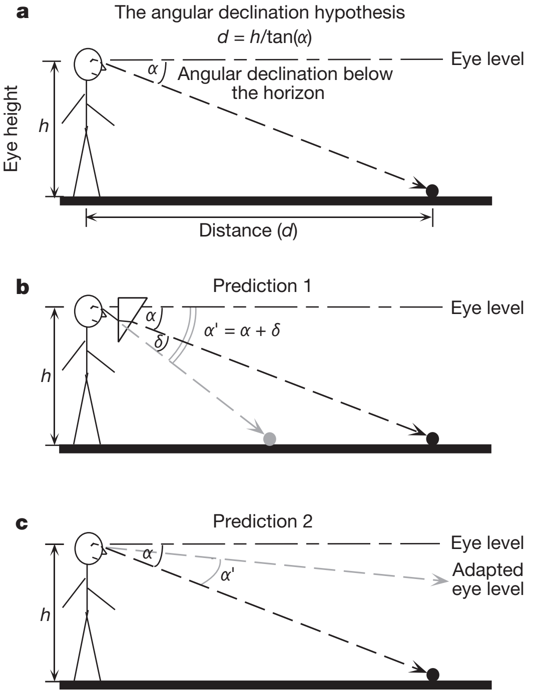

**Figure 1** The angular declination hypothesis. **a**, The hypothesis describes how the visual system can compute distance ($d$) from the eye height ($h$) and the angular declination below the horizon ($\alpha$), with the trigonometric relationship $d = h/\tan(\alpha)$. **b**, Prediction 1. A base-up prism increases the object's angular declination from $\alpha$ to $\alpha + \delta$, reducing computed distance. **c**, Prediction 2. The after-effect of base-up prism adaptation is a downward shift of the eye level. Because the eye level serves as a reference for computing the angular declination below the horizon, and the object's angular declination ($\alpha$) is reduced to ($\alpha'$), distance is overestimated.

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predict that the perceived distance will increase (Fig. 1c).

We tested both predictions using a blindfolded-walking paradigm[7–10], where an observer binocularly previews a target and then walks to the target's location in blindfold traversing the remembered target distance (a visually directed task). In our experiments, which were conducted in a well-lit visual environment, we first measured seven naive observers' baseline performances. We found that the observers performed the task quite accurately (Fig. 2a). Then, we measured the observers as they viewed through a pair of 10 Prism Diopters (PD) (5.73 degrees) base-up prisms. This time, they significantly underestimated distance (Fig. 2a) compared with the baseline condition (two-way analysis of variance (ANOVA) with repeated measures, $F = 41.053$, degrees of freedom d.f. = 1,6, $P < 0.001$). Thus, our finding confirms the first prediction of the angular declination hypothesis (Fig. 1b).

To test the second prediction (Fig. 1c), we induced prism adaptation in the same observers by having them perform purposeful walking while wearing the pair of 10 PD base-up prisms for 20 min. Thereafter, we removed the prisms and measured the observers' distance judgements (after-effect condition) using the blindfolded-walking paradigm. Their averaged walked distances are shown in Fig. 2a, which reveals distance overestimations compared with the baseline (two-way ANOVA with repeated measures, $F = 24.16$, d.f. = 1,6, $P < 0.003$), confirming our second prediction.

The second prediction was reconfirmed by a different prism-adaptation method. We adapted the same observers by having them stand still and throw beanbags to two targets on the floor (1.8 and 3.6 m) while wearing the pair of 10 PD base-up prisms for 20 min. We then measured the prism after-effect, and found the observers overestimated target distances (two-way ANOVA with repeated measures, $F = 11.65$, d.f. = 1,6, $P < 0.015$). Their results are shown in Fig. 2b, which also plots their performances in the baseline and prism conditions that were tested before the throwing-adaptation experiment. Clearly, these results are similar to those in the walking-adaptation experiment (Fig. 2a). Importantly, because the observers did not walk during the throwing-adaptation phase, we can rule out the possibility that the after-effect found with the walking-adaptation experiment was solely due to an adaptation within the walking-locomotion system (a blindfolded-walking paradigm was used to measure the perceived distance)[15].

Our findings have confirmed the two predictions of the angular declination hypothesis. This hypothesis, however, hinges on the implicit assumption that the visual system uses the eye level as a reference for computing the angular declination of the object (Fig. 1a). But while this assumption is critical, it also lacks direct empirical support. Thus, the remainder of our study was dedicated to proving that a recalibration of the eye level serves as the mechanism for deriving distance judgements, from the angular declination below the horizon. Below, we measured the impact of base-up prism adaptation on judgements of eye level and target location. Both sets of experiments were conducted in the dark to increase the reliability of the eye level measurements[16].

We first measured the observer's eye level by having the observer instruct the experimenter to locate a red light at the observer's eye level from a viewing distance of 2.4 m. Six new naive observers and

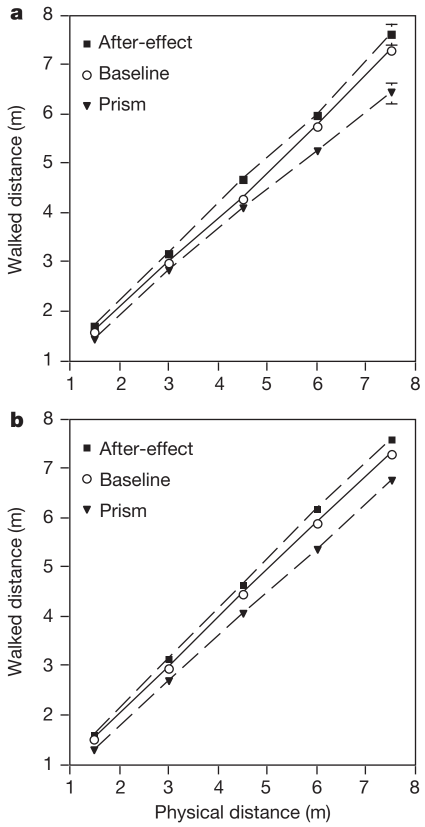

**Figure 2** The effect of viewing through a pair of 10 PD base-up prisms and the after-effect of adaptation to base-up prisms on judged distance in the light ($n = 7$). Relative to the no-prism baseline condition, observers underestimated distance when viewing through prisms, and overestimated distance after prism adaptation when measured with prisms removed. Prism adaptation was induced by (**a**) purposeful walking and (**b**) throwing beanbags.

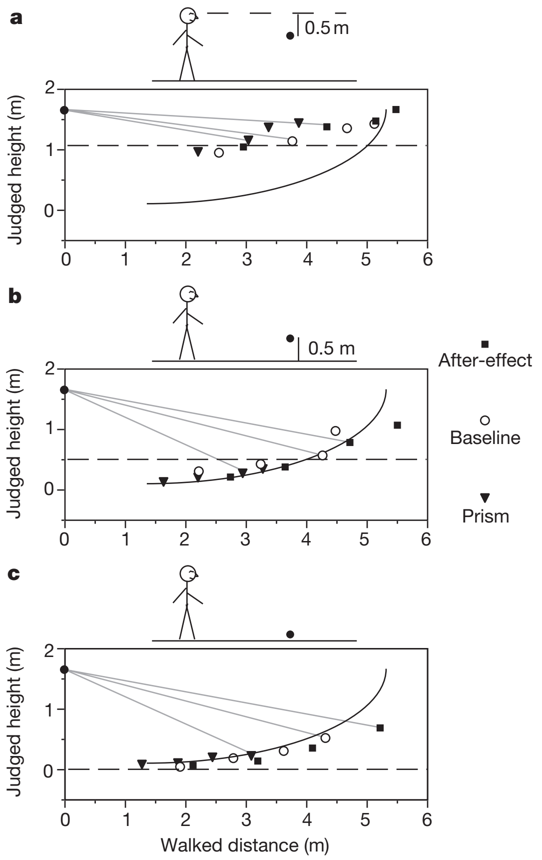

**Figure 3** Perceived locations of a dim target in the dark for the baseline, prism and after-effect conditions. The target heights (indicated by the dashed lines) were 0.5 m below eye level (**a**); 0.5 m above the floor (**b**); or on the floor (**c**). Relative to baseline, judged target location was further and higher in the after-effect condition, and nearer and lower in the prism condition ($n = 7$). This general trend is emphasized in each graph by the three grey lines, which connect the perceived target locations to the average eye positions on the $y$ axes (for the same test target in the three viewing conditions). Doing so allows us to calculate the perceived angular declination for each judged target location (Fig. 4).

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one author participated in all three conditions: baseline, prism and after-effect. To induce prism adaptation, the observers wore a pair of 20 PD (11.5 degrees) base-up prisms and walked about in the light for 20 min. Consistent with previous reports[17], the judged eye level was slightly below the physical eye level (−2.19 ± 0.57 degrees, mean ± s.d.) in the baseline condition. For the prism condition, the eye level was higher than baseline (8.20 ± 1.89 degrees), whereas it was lower than baseline in the after-effect condition (−5.00 ± 0.92 degrees). Clearly, the results indicate that the eye level can be altered by prisms.

In another experimental session, we measured the same seven observers' judgements of target locations in the dark. During a trial, the observer previewed a red light target that was randomly placed at 1 of 12 predetermined locations (4 distances × 3 heights). The observer walked the remembered target distance and gestured the target's height. Figure 3 shows the average results in three separate graphs for the three target heights tested. The graphs relate the judged target height (*y* axis) to the judged target distance (*x* axis), respectively, for the baseline, prism and after-effect conditions. Also indicated on the *y* axes are the average physical eye heights, which we connected by lines to a representative datum from each of the three viewing conditions. This allows us to illustrate the changes in perceived angular declination across viewing conditions. Overall, compared to baseline, angular declination is increased in the prism condition, resulting in significant decreases in perceived target distances ($t = 10.17$, d.f. = 11, $P < 10^{-6}$) and heights ($t = 4.66$, d.f. = 11, $P < 0.001$). Meanwhile, angular declination is decreased in the after-effect condition, resulting in significant increases in perceived target distances ($t = 7.99$, d.f. = 11, $P < 10^{-5}$) and heights ($t = -2.63$, d.f. = 11, $P < 0.025$).

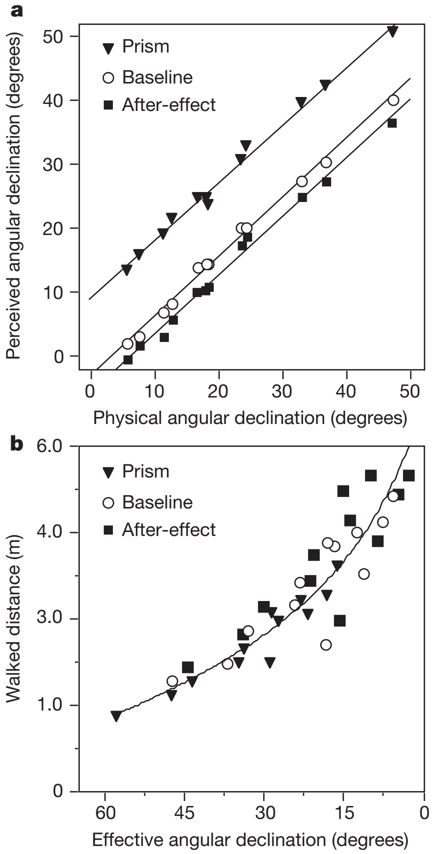

**Figure 4** Veridical judgement of angular declination and its monotonic relationship to distance. **a**, The perceived angular declination derived from Fig. 3 plotted as a function of physical angular declination below the horizon, along with the regression lines for each viewing condition. For the baseline condition, the slope of the regression line is 0.922. The slopes for the prism and after-effect conditions are 0.902 and 0.910, respectively. They are not significantly different from the baseline condition ($F = 0.411$, d.f. = 1,11, $P = 0.54$; $F = 0.275$, d.f. = 1,11, $P = 0.61$). **b**, A monotonic increase in walked distance with effective angular declination. The hyperbolic curve $d = h/[a\tan(\alpha) + b]$ was fitted to the data by the least squares method (where $d$ is distance, $\alpha$ is effective angular declination and $h$ is average eye height (1.62 m); constant a = 0.6194 and constant b = 0.2426).

The data in Fig. 3b seem to be distributed along a trend, about the curve, which we fitted by eye. We also drew the same curve in Fig. 3a and c. As can be seen, the fit is good for Fig. 3c. Thus, Fig. 3b and c suggest that in the dark, the visual system tends to treat targets on or near the floor as if they are located on a distinct curved surface[2,18]. For Fig. 3a, only data points representing further target distances fit the curve, whereas those representing nearer target distances are distributed above the curve. This is probably because of their relatively short distances from the eyes, causing their distance judgement to be affected by other near depth cues such as ocular motor, binocular disparity and motion parallax cues.

We next verified the possibility that prism adaptation affects the judgements of both distance and height, possibly stemming from a recalibration of the eye level. We calculated the perceived angular declination for the data in Fig. 3, and plotted them in Fig. 4a as a function of the physical angular declination of the targets used. A linear relationship is revealed between the perceived and physical angular declination below the horizon for all three conditions. Furthermore, the three regression lines are parallel, suggesting a constant change in angular declination. We also calculated the average difference in perceived angular declination between the after-effect and baseline conditions: −2.90 ± 0.44 degrees, which is very close to the average difference in eye level (−2.82 ± 0.74 degrees) between the after-effect and baseline conditions from the eye level judgement experiments ($t = 0.796$, d.f. = 6, $P = 0.46$). Thus, it indicates that a change in the eye level very probably affects the perceived target locations (Fig. 3). This provides compelling support for the implicit assumption of the angular declination hypothesis, that the eye level serves as a reference for computing the angular declination below the horizon.

We then performed the same analyses for the prism condition relative to baseline, wherein we found the average difference in angular declination to be 11.63 ± 1.37 degrees, and the average difference in eye level to be 10.38 ± 1.43 degrees. These also do not differ from each other ($t = 0.103$, d.f. = 6, $P = 0.92$), indicating a common basis. The differences in perceived angular declination and in eye level due to the prisms are close to 11.5 degrees, which is the physical angular deviation caused by the prisms. Such concordance legitimizes the methods we employed to obtain the measurements of eye level and angular declination.

Knowing the changes in eye levels allowed us directly to relate the walked distance to the effective angular declination for each condition. (Effective angular declination for the prism condition = physical angular declination + 10.38 degrees; effective angular declination for after-effect condition = physical angular declination − 2.82 degrees). This is plotted in Fig. 4b, which shows a monotonic function, confirming that angular declination is a depth cue[2] for distance judgement.

That eye level is not fixed but subservient to the visual environment after a short period of prism adaptation suggests the existence of a plastic mechanism that calibrates the intrinsic body information to the visual environment[12–14]. Indeed, such a learning mechanism is critical for ensuring that we correctly perceive the lawful relationship between the physical properties of the visual environment and our visuomotor system[12–15].

Our study provides direct support for the angular declination hypothesis, that the visual system can access the angular declination below the horizon to determine absolute distance. This finding is consistent with several empirical studies[19–21], such as that by Philbeck and Loomis[21] in their reduced cue condition. Our

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study reinforces this notion by relating the changes in the angular declination below the horizon to perceived eye level, and demonstrating that the eye level serves as a reference for the visual system to compute the angular declination below the horizon. ☐

## Methods

### Observers

Thirteen naive observers with informed consent and one author with self-reported normal vision participated in the various experiments.

### Blindfolded-walking paradigm in the light

The observer stood in a hallway 25 m long (starting about 10 m to one end of the hallway) and previewed a rectangular cardboard target (2.12 degrees) on the floor at one of five distances (1.5, 3.0, 4.5, 6.0 or 7.5 m). The observer then wore a blindfold and walked the remembered distance in the direction of the target (which had been removed). When the judged distance was reached, the experimenter measured it, and then led the observer in blindfold to the starting point to begin a new trial (no feedback was provided). Each target distance was measured twice (counterbalanced).

### Blindfolded-walking paradigm in the dark

The observer stood in a dark room and previewed an internally illuminated red table-tennis ball (target, 0.16 cd m$^{-2}$) at one of four distances (1.5, 2.5, 3.75 or 5.0 m) and three elevations (on the floor, 0.5 m above the floor, or 0.5 m below the eye). The target was then removed for the observer to begin walking in the dark, traversing the remembered target distance. On reaching the destination, the observer gestured the remembered target elevation with his/her left hand. No feedback was given to the observer. Each target location was randomly selected and measured twice. All targets viewed from the same distance had the same physical size, which subtended 0.23 degrees at the eye level.

### Prism-adaptation method

The observer wore a pair of base-up prism goggle (10 PD (5.73 degrees) or 20 PD (11.5 degrees) from Bernell/USO) for 20 min, while actively performing one of two tasks: walking about, with the specific instruction to navigate complex obstacle courses in the natural visual environment; or standing still and throwing beanbags to a target on the floor 1.8 or 3.6 m using the right hand. To maintain the after-effect of prism adaptation during our lengthy experiment when measuring target locations in the dark, the observer wore the prisms in a lighted room between trials.

### Judging eye-level task

In a dark room, the observer stood still with his/her head held by a head and chin rest. A red light target (supported by a wall) that subtended 0.23 degrees was moved by the experimenter from a viewing distance of 2.4 m from the observer, who would instruct the experimenter to stop moving the light when it was perceived to be at the observer's eye level. The procedure was repeated five times for each condition tested.

Received 20 July; accepted 20 September 2001.

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**Acknowledgements**

We thank K. A. May and P. J. Gunther for their assistance in collecting the data in the first experiment. This research was supported in part by grants from the Knights Templar Eye Foundation and the Southern College of Optometry (to T.L.O.) and a Competitive Enhancement Grant from the University of Louisville (to Z.J.H.).

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# Linear processing of spatial cues in primary auditory cortex

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**To determine the direction of a sound source in space, animals must process a variety of auditory spatial cues, including interaural level and time differences, as well as changes in the sound spectrum caused by the direction-dependent filtering of sound by the outer ear[1]. Behavioural deficits observed when primary auditory cortex (A1) is damaged have led to the widespread view that A1 may have an essential role in this complex computational task[2–5]. Here we show, however, that the spatial selectivity exhibited by the large majority of A1 neurons is well predicted by a simple linear model, which assumes that neurons additively integrate sound levels in each frequency band and ear. The success of this linear model is surprising, given that computing sound source direction is a necessarily nonlinear operation[6–9]. However, because linear operations preserve information, our results are consistent with the hypothesis that A1 may also form a gateway to higher, more specialized cortical areas[10,11].**

The ability of many species to pinpoint the direction of a sound source both in azimuth and elevation with an error that may be as little as a few degrees is remarkable, considering the complex and ambiguous nature of the acoustic information available to solve this task. Animals must combine spatial information provided by different acoustic cues, including time-of-arrival and level differences in the signal received at each ear, as well as changes in the spectrum of the signal generated by direction-dependent filtering of the sound by the head and external ears. Individually, these cues suffer from inherent ambiguities. For example, within a given narrow frequency band, a number of source directions can generate identical interaural time and level difference values[12]. Similarly, the filtering by the external ears convolves, and thus confounds, spectral localization cues with the source spectra[13,14]. Consequently, the central auditory system must extract, process and combine information over many frequency channels and from both ears to achieve the highly accurate localization performance exhibited by many species. The fact that damage to A1 in mammals produces marked, and specific, deficits in auditory localization performance[2–5], may mean that A1 has a critical role in the pathways underlying spatial hearing and may be responsible for performing many of the computations that underlie the perception of sound source location. Indeed, the most clearly documented behavioural impairment observed following a unilateral lesion of the auditory cortical areas, including A1, is an inability to localize sounds on the side opposite the lesion[2–5,15].

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