
The myth of upright vision. A psychophysical and functional imaging study of adaptation to inverting spectacles

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Abstract. The adaptation to inverting prisms and mirror spectacles was studied in four subjects over periods of six to ten days. Subjects showed rapid adaptation of visuomotor functions, but did not report return of upright vision. The persistence of the transformed visual image was confirmed by the subjects' perception of shape from shading. No alteration of the retinotopy of early visual cortical areas was seen in the functional magnetic resonance images. These results are discussed in the context of previous claims of upright vision with inverting prisms and mirror spectacles.

1 Introduction

The psychology of perception produced few dogmas more deeply entrenched in the general mind than the return of upright vision during adaptation to inverting spectacles. Stratton's (1897) claim that he saw the world in its canonical orientation on the sixth day with inverting prisms was followed by attempts to reproduce his findings in 1928 and 1952 (see Kottenhoff 1961; Gregory 1998b). A number of studies at Innsbruck University with upside-down inverting mirrors (Kohler 1964) also resulted in reports of upright vision after one week. These alleged perceptual changes occurred concomitantly with the improvement of motor functions. On the other hand, the introspective data from a series of Japanese visual transposition experiments, conducted on a similar time scale, suggested that throughout the experiments the awareness of visual transposition remained stronger than the sense of reality of the new vision (Yoshimura 1996). Thus, more than 100 years after Stratton's report, the controversy that arose from his claims is "still unresolved" (Gregory 1998b).

The interest in visual inversion and distortion experiments was recently fuelled by the opportunity to investigate mechanisms of oculomotor and visuomotor adaptation at the single-cell level. Left–right reversing prisms lead to a rapid change in the gain of the vestibulo-ocular reflex (Melvill Jones and Gonshor 1982; Melvill Jones et al 1988), which has been associated with altered response properties of neurons in the flocculus (Lisberger and Fuchs 1978; Lisberger et al 1994). Sugita (1996) studied the adaptation to left–right reversing prisms in monkeys and reported that, after six weeks, 43 out of 119 cells recorded from VI were found to respond to ipsilateral as well as contralateral stimulation. These cells, however, had no preference for orientation or direction of motion, which suggests deterioration of function rather than compensation. The limited adaptability of early visual areas is also documented by experiments in kittens and adult cats that experienced a rotated visual field following cyclotorsion of the eyes. Neither the developing nor the adult cats were able to adjust behaviourally to the distorted visual input and within a few days developed a near-complete neglect of the visual modality. This neglect was associated with a remarkable loss of responsiveness and response selectivity in neurons of the primary visual cortex (Singer et al 1979a, 1979b, 1982a). In adult cats, these neuronal modifications were reversible when normal vision was restored (Singer et al 1982b), but no similar effect was observed in kittens.

Thus, in early visual areas distortions of retinal coordinates do not appear to lead to compensatory readjustments but rather to dedifferentiation, as postulated by Fiorentini et al (1972). Truly compensatory processes seem to be confined to higher visual and visuomotor areas, particularly in the parietal cortex. Clower et al (1996) studied the gradual improvement of visually guided movements of human subjects whose visual input was distorted by prism spectacles, and found increased regional cerebral blood flow in the contralateral posterior parietal lobe during the adaptation.

Little, if any, attention has been paid to the question whether the motor adaptation that occurs during the wearing of inverting spectacles is indeed matched by a concomitant perceptual adaptation. We therefore performed a series of experiments with inverting prisms and mirror spectacles on human subjects in order to try and reproduce the earlier reports of return of upright vision and identify the underlying neuronal mechanisms using functional magnetic resonance imaging (fMRI).

2 Methods

Four healthy right-handed volunteers took part in the experiment (age range 20–28 years, mean 25 years, all male). Written informed consent was obtained from all subjects and appropriate measures for their safety taken. Subjects were monitored round the clock during the experiment. One subject (author DL) wore a pair of inverting prisms (rotation through 180° ; prism system custom-made by Carl Zeiss Augenoptik, Aalen) for ten days, exactly replicating the duration and the optical inversion mechanism of Stratton's (1897) experiment, with the exception that a binocular mechanism was used (the system was adjusted for far targets, but the left prism could be covered during the exploration of the near environment). The three others (co-authors UK and AH, and subject DK) wore a custom-made upside-down inverting mirror of the type used in the Innsbruck experiments (see figure 1) for seven, eight, and ten days, replicating the optical mechanism and duration of the pioneering mirror experiments of Kundraitz and Marte carried out in 1947 (see Kottenhoff 1961). During the experiment subjects had no visual input other than through these optical devices (or similar devices mounted on the MRI head coil). Eyes were blindfolded at night. Subjects had to perform their everyday tasks with as little help as possible. The days were filled with tests in the institute, walks, visits to the zoo or the museum, and other recreational activities.



Figure 1. Subject DK wearing the upside-down inverting optical system. The visual field of the subject does not extend beyond what is seen through the mirror. The maximum visual field is 85 deg wide and 22 deg high.

2.1 Behavioural tasks

The daily programme in the institute included the following psychophysical tests:

(a) Reading of inverted and normal phrases. Subjects were shown 198 phrases in blocks of 24 each, half of which were presented in conventional orientation. The other half were presented in the respective transformation, ie inverted or upside down. Subjects were requested to make a syntactic decision (phrase or pseudophrase), and their reaction times were measured. The same sentences were used each day in order to study the differential effects of item-specific facilitation for letter strings in conventional and transformed orientation. This task was based on the mirror-reading task, examined psychophysically by Kolars (1968, 1975, 1976) and in two recent fMRI studies (Goebel et al 1998a; Poldrack et al 1998).

(b) Perception of shape from shading. We used a stimulus described by Ramachandran (1988), presenting a central target circle that was surrounded by six circles with an opposite contrast distribution. Subjects had to decide whether the perceived hemisphere pointed inward or outward ('eggs': figure 2a). As a second shape-from-shading stimulus we used squares that were composed of two neighbouring bright edges and two dark edges ('squares': figure 2b). These squares evoke the illusion of buttons. Subjects had to decide whether the buttons pointed inward or outward. These stimuli rely on the reversal of depth perception that is brought about by shifting the light source of cast shadows from above to below (Gregory 1998b). This extraction of 3-D shape from shading depends on retinal rather than gravitational cues and is assumed to be carried out early in visual processing (Kleffner and Ramachandran 1992). This effect is not known to become more labile with repetition.

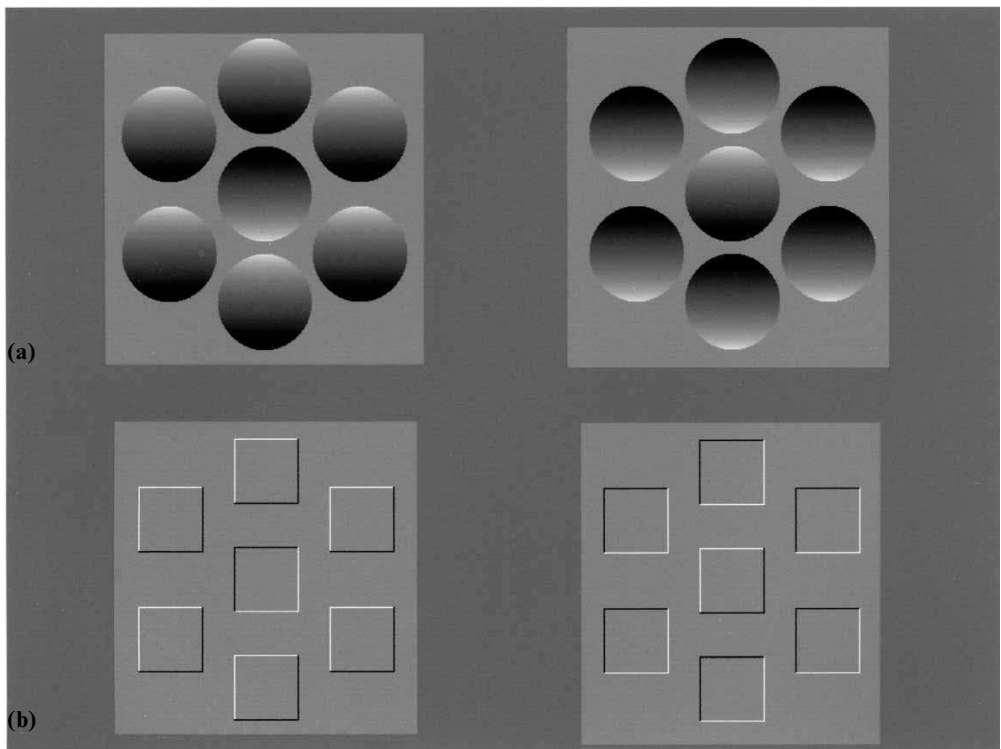


Figure 2. The stimuli for the extraction of three-dimensional shape from shading. (a) A central target circle is surrounded by six circles with the opposite contrast distribution. Subjects report whether they perceive the central stimuli as eggs or cavities. (b) The squares are composed of two neighbouring bright edges and two dark edges. Subjects decide whether the buttons point inward or outward.

(c) Building three-dimensional objects. Subjects had to copy three-dimensional objects of four, six, and ten components with a set of building bricks, and their response times for correct completion of the task were recorded. New objects were presented each day in order to minimise the effect of item-specific facilitation and maximise that of visuomotor skill learning.

2.2 Functional magnetic resonance imaging (fMRI)

The stimulus for fMRI retinotopic mapping was a checkerboard disk segment subtending 45 deg of visual angle, which rotated clockwise starting at the left horizontal meridian (360° in 96 s; see figure 3). The stimulus was optimised for reliable mapping of the four visual quadrants (rather than the borders of early visual areas). Each mapping experiment consisted of four repetitions of a full rotation and was performed every day (DL) or every other day (UK, AH, DK) at 1.5 T (Siemens Magnetom Vision) with the use of the standard head coil and a gradient echo EPI sequence. The Siemens Magnetom gradient overdrive allowed functional scans with high spatial and temporal resolution (1 volume = 12 axial slices; TE = 69 ms, FA = 90° , TR = 3000 ms, FOV = 210×210 mm², voxel size $1.6 \times 1.6 \times 3.0$ mm³) to be made. Retinotopy of polar angle was revealed with cross-correlation analysis. After the selection of a 45° reference wedge of the visual field, the blood-oxygen-level-dependent (BOLD) time course of fMRI was correlated with

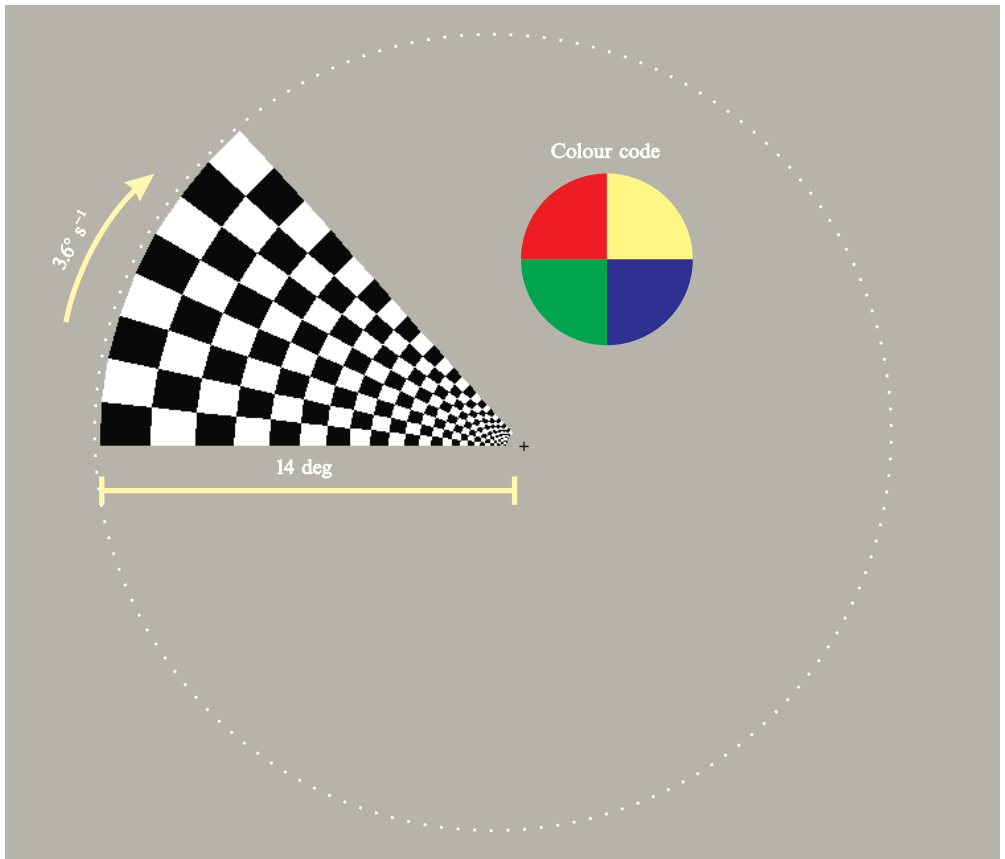


Figure 3. The stimulus for fMRI retinotopic mapping. A checkerboard disk segment subtending 45 deg of visual angle rotated clockwise starting at the left horizontal meridian (360° in 96 s). Quadrant colours in the disk correspond to colouring of lag values of the cross-correlation maps (see figures 5 and 6, and also <http://www.perceptionweb.com/perc0499/linden.html>).

an ideal response function that assumes a value of one for the 12 s during which the checkerboard covers only the reference section (corrected for a haemodynamic delay of 4 s) and zero for the remaining 84 s of each cycle. For each voxel in the retinotopic cortex, the lag of the maximum correlation then denotes the polar angle with respect to the reference section. Lag values were colour-coded and used to compute 2-D cross-correlation maps.

2-D statistical maps were converted into polychromatic images, superimposed on the 2-D anatomical images and incorporated into 3-D T1-FLASH (fast low-angle shot) data sets, which were obtained in the same scanning session, through interpolation to the same resolution (voxel size: $1.0 \times 1.0 \times 1.0 \text{ mm}^3$). This allowed us to superimpose 3-D statistical maps onto the 3-D anatomical data sets. Since the 2-D functional and 3-D structural measurements were performed within the same recording session, coregistration of the respective data sets could be computed directly on the basis of the Siemens slice position parameters of the T2*-weighted measurement (number of slices, slice thickness, distance factor, Tra – Cor angle, FOV, shift mean, off-centre read, off-centre phase, in-plane resolution) and on parameters of the 3-D T1-FLASH measurement (number of sagittal partitions, shift mean, off-centre read, off-centre phase, resolution) with respect to the initial overview measurement (scout).

For each subject, the structural 3-D data sets were transformed into Talairach space. Talairach transformation was performed in two steps. The first step consisted in rotating the 3-D data set of each subject to be aligned with the stereotaxic axes. For this step the location of the anterior commissure (AC) and the posterior commissure (PC) and two rotation parameters for midsagittal alignment had to be specified manually in the 3-D T1-FLASH data set. In the second step the extreme points of the cerebrum were specified. These points together with the AC and PC coordinates were then used to scale the 3-D data sets into the dimensions of the standard brain of the Talairach and Tournoux atlas (Talairach and Tournoux 1988) by a piecewise affine and continuous transformation for each of the 12 defined subvolumes. The individual Talairach 3-D maps were averaged across subjects and superimposed on a normalised anatomical 3-D data set. Prior to averaging, the functional 3-D maps were smoothed with a Gaussian kernel of 5 mm FWHM.

The high-resolution T1-weighted 3-D recordings of the three subjects AH, DL, and UK were used for surface reconstruction of both hemispheres. The white/grey matter border was segmented by a region-growing method. In order to improve the intensity-based differentiation of grey and white matter, a 3-D sigma-filter was applied. This nonlinear filter smooths the data within each tissue type without blurring the transitions between them. Manual cuts in the midbrain (setting intensity values to zero) prevented the cerebellum and the eyeballs from being included in the region growing. Additionally, some subcortical structures were manually labelled as belonging to 'white matter' in order to exclude them from the cortical reconstruction process. The two resulting segmented subvolumes were tessellated to produce a surface reconstruction of each cortical hemisphere. Tessellation consisted in defining two triangles for each side of a voxel located at the border of the segmented volumes. Additionally, all nearest neighbours of each individual vertex were determined and explicitly stored to allow efficient 3-D morphing operations. The tessellation of a single hemisphere typically consists of approximately 240 000 triangles. The reconstructed surface of the cortical sheet of each hemisphere was subjected to iterative corrective smoothing (100–200 iterations). An iterative 3-D morphing algorithm (Goebel et al 1998b) was used to let the surface grow smoothly into the grey matter. Through visual inspection, this process was halted when the surface reached the middle of grey matter corresponding approximately to layer 4 of the cortex. The resulting surface was used as the reference mesh for the projection of functional data on folded, inflated, or flattened representations.

Inflated representations of the cortical sheet were obtained by applying several hundred smoothing iterations of the morphing algorithm. A morphed surface always possesses a link to the folded reference mesh so that functional data can be shown at the correct location of a (partially) inflated as well as flattened representation. This link was also used to keep geometric distortions to a minimum during inflation and flattening through the inclusion of a morphing force that keeps the distance between vertices and the area of each triangle of the morphed surface as close as possible to the respective values of the folded reference mesh (cf Van Essen and Drury 1997). The flattening of the cortical surface was prepared by manually removing remaining subcortical structures and applying 4–5 radial cuts on the medial surface of an inflated hemisphere. The surface was then projected into a sagittal image plane in one step. An iterative process was then applied to move the triangles on the medial side radially outward. If during this process a triangle reaches the border of the medial to the lateral side, it is ‘flipped’ to become an ‘outside’ triangle that now belongs to the lateral side. This process fully converts all ‘inside’ triangles to ‘outside’ triangles after several hundred iterations (300–500). The resulting fully flattened hemisphere is finally subjected to the correction forces until the distortion error is less than 15%. The full process of segmentation, reconstruction, inflation, and flattening lasts typically less than 2 h on a 500 MHz DEC Alpha workstation. Since in the polar-mapping experiment we were only interested in possible changes in the mapped early visual areas, only a part of the occipital lobes of both hemispheres was finally cut and used for visualisation. The resulting flat maps provide clear representations of the topographical relationships in visual cortex (cf Sereno et al 1995; Tootell et al 1996).

In order to obtain a quantitative measure of the stability of retinotopic representation during the adaptation to inverting spectacles a retinotopic stability coefficient RSC was computed (table 1). The analysis of a polar-mapping experiment results in 24 colour-coded lag values (6 for each quadrant), each representing part of the visual field (polar angle). A single vertex of the flattened surfaces may assume a lag value (colour) on day b (lag_{db}) as well as on day a (lag_{da}). If $\text{lag}_{\text{da}} - 2 \leq \text{lag}_{\text{db}} \leq \text{lag}_{\text{da}} + 2$, the vertex is counted as ‘stable’. If lag_{db} falls outside that range, the vertex is regarded as unstable. The retinotopic stability coefficient is defined as $\text{RSC} = S/N$ where S denotes the number of all ‘stable’ vertices and N denotes the number of all vertices of both hemispheres that possess a significant lag value on both measurement days. Note that the range of ± 2 lags of a total of 24 lags comprises a very conservative criterion. In the case of a true retinotopic reversal, the stability index should have a value close to 0. If, instead, no

Table 1. The retinotopic stability coefficient (%) for the left (*L*) and right (*R*) hemispheres alone and for the unweighted mean of the two hemispheres, which reveal a high degree of stability during the experiment: for subject AH, experimental and post-experimental versus baseline; for subjects DL and UK, experimental versus baseline.

	<i>L</i>	<i>R</i>	$\frac{1}{2}(L + R)$
Subject AH			
day 1	86	84	85
day 3	83	87	85
day 5	78	73	75.5
day 7	88	85	86
post-exp.	82	92	87
Subject DL			
day 7	71	68	69.5
Subject UK			
day 4	67	62	64.5

change in retinotopic representation occurs, the value should be close to 1 (100%). Yet even in the latter case a value of 100% can only be expected in the absence of inter-measurement variability.

3 Results

All subjects showed a rapid adaptation of motor skills. On the third day of the experiment, they were capable of walking freely without a stick. Subjects performed all tasks of everyday life with none or minimal aid. During the second half of the experiment, they were able to find their way in a crowded department store and to ride a bicycle. The execution of very fine movements, however, was slowed down and remained so until the end of the experiment. For instance, the building of three-dimensional objects still took twice the baseline time on the last day of the experiment (figure 4).

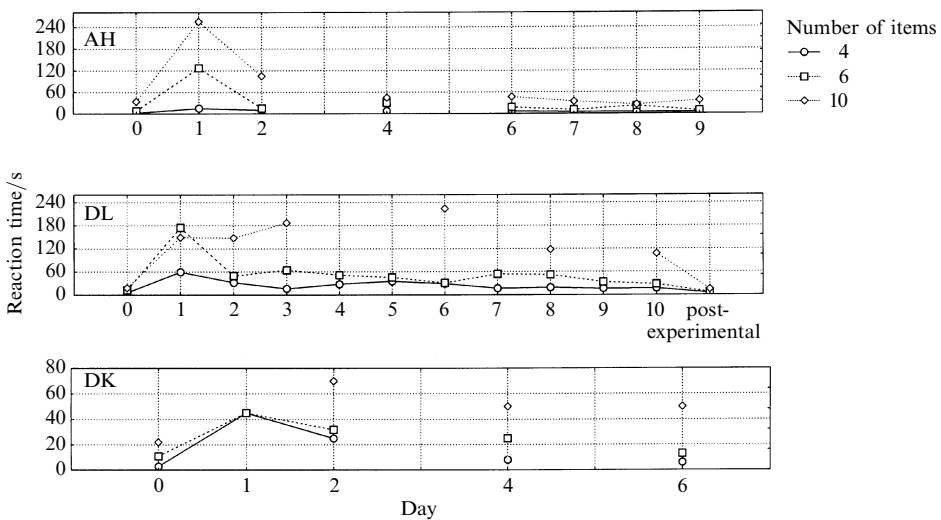


Figure 4. Visuomotor performance (object building from four, six, and ten items) of subjects AH, DL, and DK. During the first days of the experiment motor performance was markedly worse than pre-experimentally (day 0). The degree of subsequent motor adaptation varied substantially between individuals. Note that subjects AH and DK did not perform this task on a daily basis. If only the ten-item reaction time is missing, no correct execution of the task could be observed on that day.

In experiments with an inverting mirror it took four days until subjects were able to read the clock correctly. Subjects were barely able to write in a conventional orientation on the first day, but improved quickly. One subject even wrote daily letters. Reading of phrases in conventional orientation improved markedly during the experiment, but reaction times remained above those for inverting mirror reading until the spectacles were taken off (see figure 7).

In the shape-from-shading task, one subject showed increasing ambiguity from day 5 onwards (ie 75% of the responses were compatible with the conventional orientation), but the responses of the others remained in accordance with the transformed orientation throughout the experiment (figure 8).

The subjects reported that at times they had the impression that they themselves, rather than the world around them, had been turned upside down, but that they knew that this was not the case. But no subject claimed that he had regained upright vision or that his visual image matched his body sense at any point during the experiment, not even when the subjects were exploring the visual scene by touch [on the rôle of tactile exploration in the previous accounts of adaptation to mirror vision see Gregory (1997)].

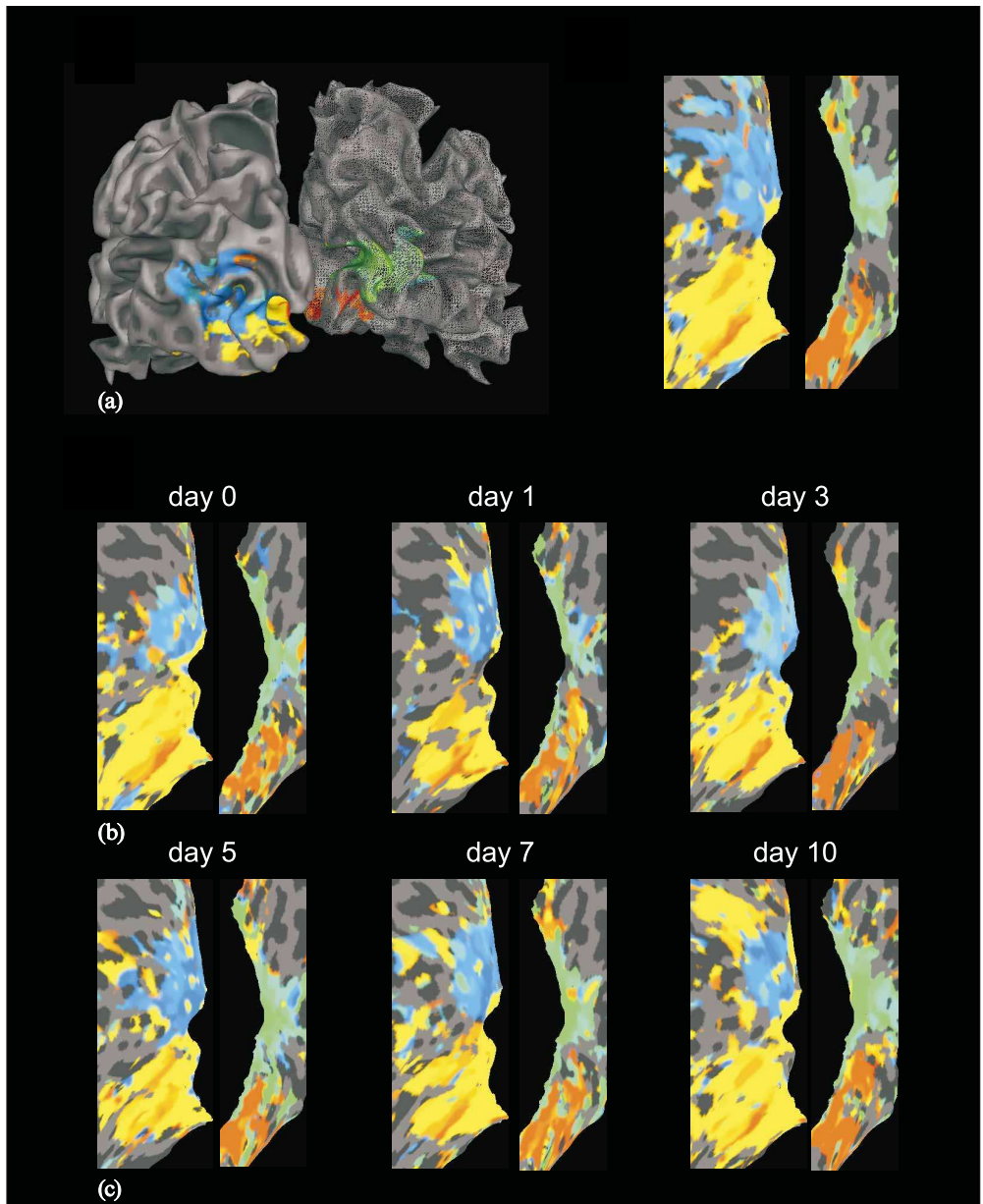


Figure 5. Results of the retinotopic polar-angle mapping of cortical areas V1, V2, and V3/VP (area borders not shown) of subject AH during the mirror experiment. (a) Posterior view of the reconstructed surface (white/grey matter border) of the posterior portions of both hemispheres of the subject's brain. The right side shows the resulting mesh of the reconstruction of the right hemisphere. The left side shows a shaded rendering of the left hemisphere. The average of the polar-angle maps of days 0 (baseline), 1, 3, 5, 7, and 10 (post-experimental) of the mirror experiment is projected onto the reconstructed surface ($r > 0.33$). Responses to stimulation in the right upper visual field are coded yellow (horizontal meridian, hm) to orange (vertical meridian, vm), in the right lower visual field blue (hm) to turquoise (vm), in the left upper visual field red (hm) to orange (vm), and in the left lower visual field green (hm) to turquoise (vm). (b) Cortical flattening of the posterior part of the occipital lobe with superimposed average retinotopic maps [as in (a)]. (c) The same view as in (b). Polar-angle maps are shown for days 0, 1, 3, 5, 7, and 10 ($r > 0.33$ for all maps). The topography of retinotopic visual cortex, as indicated by the colour code, remained stable throughout the experiment.

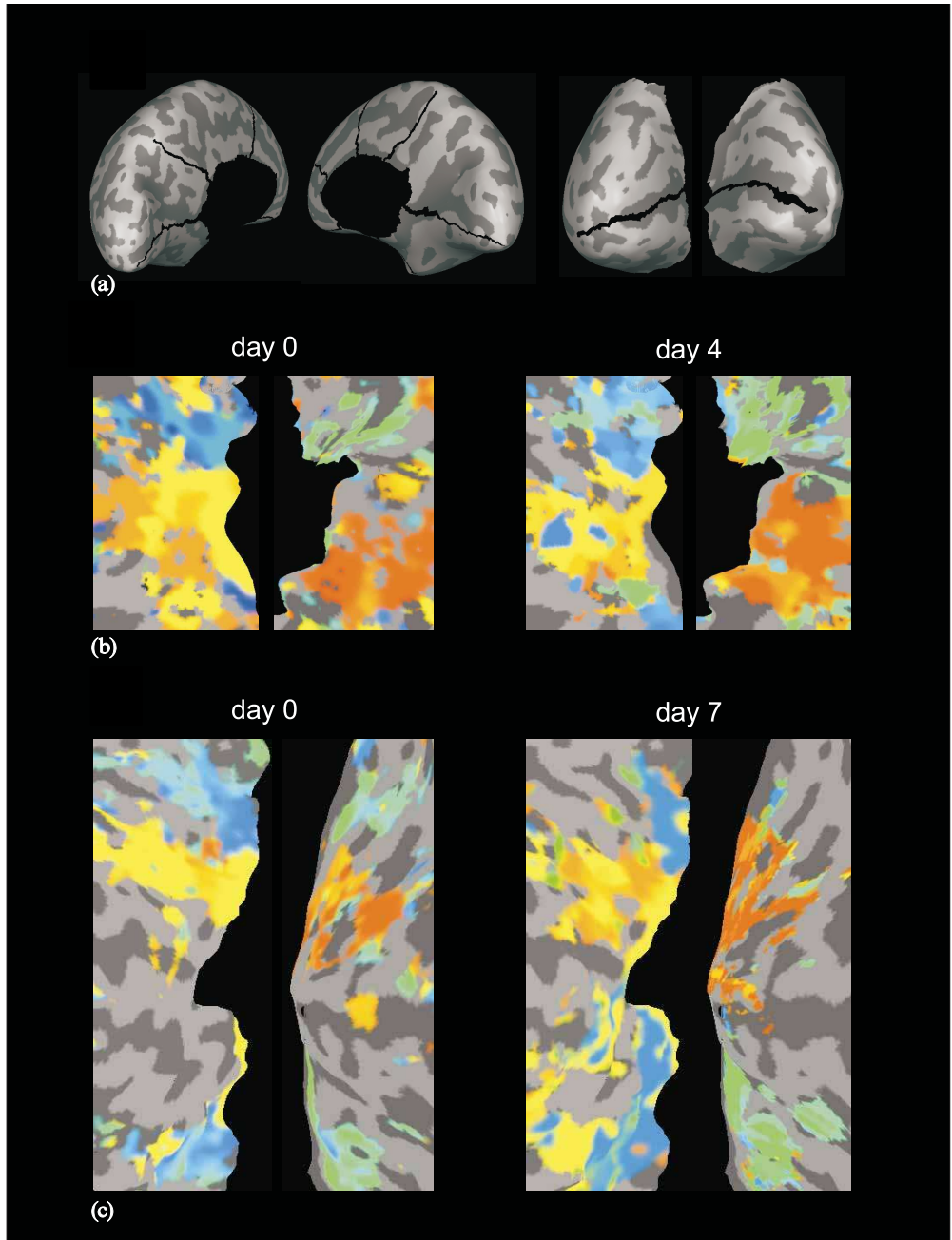


Figure 6. (a) Left side: inflated hemispheres of subject UK. The cut (for flattening) in the occipital lobe was located at the functional border between dorsal and ventral V1 (map not shown). Right side: posterior part of the inflated hemispheres of subject DL. The cuts follow the anatomical landmark of the calcarine sulcus. (b) and (c) Cortical flattening of the posterior part of the occipital lobe with superimposed retinotopic maps of subjects UK (b) and DL (c) before and late in the experiments. The topography of retinotopic visual cortex, as indicated by the colour code, remained stable throughout the experiment.

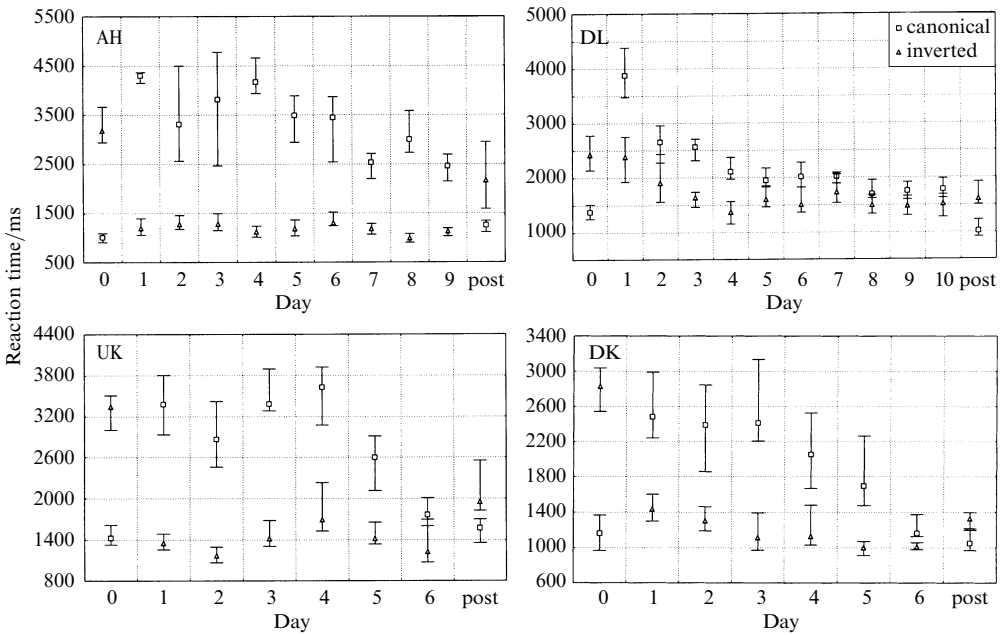


Figure 7. Reading performance of the four subjects (median: Whisker 25%, 75%). Reaction times (syntactic decision) for canonical presentation of phrases (noncanonical retinal input through mirror inversion) improved gradually during the experiment (days 1–6/9/10) but remained higher than for inverse presentation (canonical retinal input through mirror inversion). This indicates that the canonically presented phrases were still perceived to be oriented noncanonically on the last day of the experiment. The post-experimental (post) data for the canonical presentation show a return to the pre-experimental baseline (day 0), while the learning effect for the non-canonical retinal input is preserved.

Subjects felt dizzy for the first few hours with the inverting mirror spectacles, and dizziness returned for about half an hour when they had taken off the spectacles at the end of the experiment. This was the only abnormal aftereffect that the return to normal vision had on the subjects. They did not show any difficulty in readjusting to the conventional view of the world. The functional magnetic resonance images showed no change of the retinotopy of the primary visual cortex from baseline levels during the experiment (figures 5 and 6). Retinotopic stability remained high throughout the experiment with RSCs of 64.5%–86%, which reflects the residual effect of intermeasurement variability rather than systematic remapping.

4 Discussion

Our four subjects showed a visuomotor adaptation to prism- and mirror-inverted vision that was similar to that reported in previous studies (Kottenhoff 1961). Yet the results of the perceptual tasks and the subjects' reports about their experience suggest that this visuomotor adaptation did not rely on a return of upright vision. Their rapid behavioural adaptation to the new spatial structure of the visual image might have to be explained by the learning of new motor patterns and increased skill at spatial transformations (Held and Freedman 1963) rather than an adjustment of the perception of the world, seen through the mirror or prism, to the conventional orientation.

The fact that none of our subjects reported upright vision during the experiment is in keeping with parts of the previous literature. Of the five classical experiments with inverting spectacles, only two (Stratton 1897; Snyder and Pronko 1952) resulted in reports of upright vision of some sort. In the three other cases, visuomotor adaptation

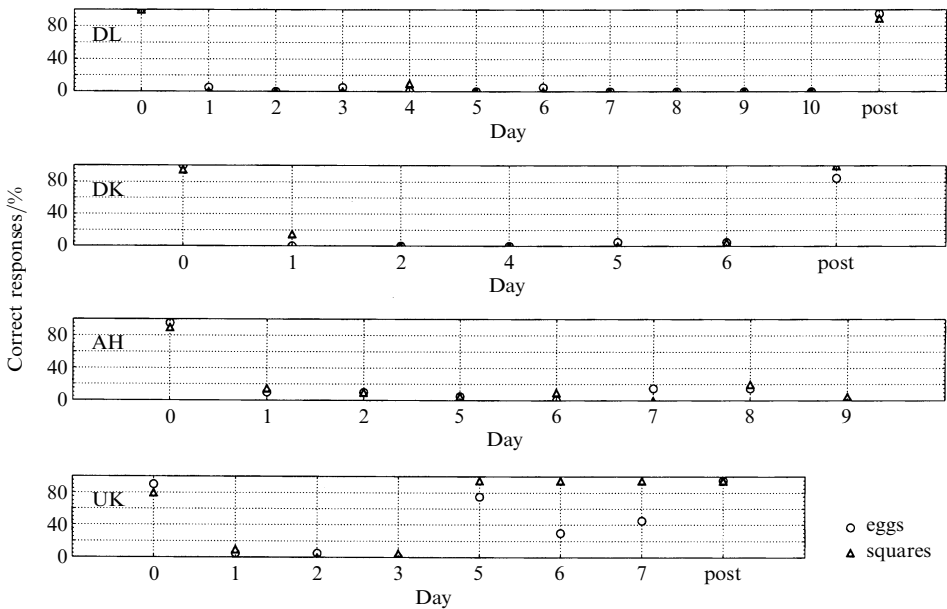


Figure 8. The extraction of three-dimensional shape from shading was determined by the orientation of the light source relative to retinal coordinates during the entire experiment in three out of four subjects. This indicates that, contrary to Stratton's (1896, 1897) assumption, adaptation to inversion or reversal of the visual field is not accompanied by a post-retinal mechanism that reverts non-canonical input to its canonical orientation. This figure shows the performance (percent correct) in the two shape-from-shading tasks ('eggs' and 'squares'). The correctness of the response was judged by the direction of the light source as presented, ie 'false' responses during the experiment indicate mirror inversion of the perceived image. Only subject UK showed a partial switch of the perceived orientation during the experiment (from day 5), but responses remained ambiguous. The post-experimental performance showed a return to baseline levels.

occurred without major changes of perception (Ewert 1928, reported in Kottenhoff 1961). The five subjects who wore upside-down inverting mirrors at Innsbruck University for periods of five days to two weeks during the years 1947–1954 all showed rapid and partly spectacular motor adaptation, including the ability to ride a bicycle or to go skiing. Around day 3 of the experiment they reported an increasing ambiguity of the visual image. Sometimes they would see an object upside down, sometimes in its conventional orientation, depending on the context and the extent to which the violation of gravity was felt to interfere with the visual image. These effects can be described as an interpretation of the visual image guided by previous knowledge about the external world and information about one's own position in it rather than fully fledged upright vision (Kottenhoff 1961). Even Stratton himself, who otherwise gave the least ambiguous account of perceptual changes, conceded the importance of the appropriate "mental attitude of the observer toward the present scene" (Stratton 1896). It is also worth considering that none of the previous investigators tested their subjects' claim to upright vision with context-independent tasks, such as the reading and shape-from-shading task used in our study.

Knowledge about the neural mechanisms and the brain regions, particularly in the parietal lobe, involved in visuomotor adaptation and visuospatial transformations, comes from lesion studies, recordings in behaving animals (Colby 1998), and functional imaging experiments on humans (Goebel et al 1998a; Poldrack et al 1998). The adaptation of visually guided reaching to the distortion of visual input by prism spectacles leads to an activation of the contralateral posterior parietal cortex (Clower et al 1996). In a previous study, we were able to identify a region in the intraparietal sulcus that is involved in the spatial transformations required for mirror reading (Goebel et al 1998a).

The parietal cortex thus has a prominent rôle in the visuospatial processing that is needed for the correct execution of reading and motor tasks during mirror-inverted vision. In agreement with the results of previous electrophysiological studies on the effects of inverted vision (Singer 1979a, 1979b, 1982a, 1982b; Yinon 1982) there was no evidence for a remapping of retinal coordinates in early visual areas. Whether other, more subtle changes, such as reduced excitability or tuning of neurons, took place cannot be decided because these parameters could not be measured with fMRI. However, the rapid recovery of normal function after restitution of normal vision seems to exclude any major modifications of basic functions in lower visual areas.

5 Conclusion

Subjects, who wore prism- and mirror-inverting spectacles over periods of six to ten days, showed a rapid visuomotor adaptation and were able to interact correctly with the surrounding world after a few days. This adaptation was not accompanied by a return of upright vision, as assessed by introspection, reading performance, and the extraction of three-dimensional shape from shading; nor was any change in the retinotopy of early visual areas observed in the functional magnetic resonance images. This dissociation of visuomotor and perceptual adaptation contradicts established views about the changes brought about by inversions of visual input. It does, however, confirm an analysis of the inversion studies that regards the reports of upright vision as referring to reinterpretations of the inverted visual image rather than genuine inversions of the orientation of the perceived image. Furthermore, interindividual differences might determine the direction of these adaptative processes. One of our subjects showed increasing ambiguity in his interpretation of shape from shading during the experiment, but never experienced a return of upright vision.

Since Stratton's first reports, psychologists and physiologists alike have been searching to explain the ability of the adult brain to reverse the visual world within one week in order to restore upright vision. Like Leonardo da Vinci in his quest for the second crossing (see Gregory 1998a; Linden 1998), they might have been pursuing yet another mythical mechanism.

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