

## ADAPTIVE CHANGES IN PERCEPTUAL RESPONSES AND VISUOMANUAL COORDINATION DURING EXPOSURE TO VISUAL METRICAL DISTORTION

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**Abstract**—The abilities of the human visual system to perform metrical judgements (comparison of lengths, estimation of angles...) involve the existence of some geometrical structure in the visual perceptual space. The question arises whether this geometrical structure is rigidly determined or is subject to adaptive changes. We have tried to answer the question by using a paradigm in which subjects are exposed to a vertically lengthened visual world and then asked to compare simultaneously presented lengths and to evaluate angles between two lines. Their perceptual responses clearly indicate a plastic adaptation to the deformed environment, though the adaptation was never complete after several days of continuous exposure to strong (25%) lengthening. For a maximum time of exposure of 7 days the rate of adaptation was found to be roughly independent of the initial degree of optical distortion. Visuomanual coordination was also investigated in these subjects, but the responses were less conclusive in this case, because of the high inter-subject variability.

Geometry of vision    Adaptation    Distorting lenses

### INTRODUCTION

The nature of the relationship between geometry and vision is of fundamental interest for the study of interactions between man and the environment. Indeed, most elementary geometric concepts issue directly from immediate properties of our visual perception. Analyzing the development of people born blind, Jeannerod (1975) showed that some geometric concepts cannot be learned or understood without the help of some kind of sensory image; this suggests that substituting tactile image techniques for vision (Bach-y-Rita, 1972) can be very useful. Among the various geometric properties of the visual system, the study of the internal representation of *metrical* parameters and operators allows a quantified evaluation of the visual system considered as a geometric object. For instance the characteristics of subjective length, distance, size, and angles provide some insight into the metrical properties of the visual system (Piaget, 1975; Wagner, 1985). Particular attention has been paid to the problem of the immersion of retinal images in three-dimensional space (Ullman, 1979).

The determination of the three-dimensional motion and structure of a monocularly viewed object is generally supposed to rely on the

assumption of local rigidity, or the principle of spatial constancy, which postulates that the central nervous system interprets any image deformation in terms of motion in depth, either rotation or translation (Gibson, 1966; Longuet-Higgins and Prazdny, 1980; Johansson, 1977; Droulez, 1985). This hypothesis, which is strongly supported by psychophysical evidence (Wallach and O'Connell, 1953; Johansson, 1978; Todd, 1984), implicitly assumes that any changes in retinal length and angle can be accurately measured by the visual system, although such measurements only constitute intermediate steps in visual metrical judgments.

The existence of metrical operators in sensorimotor control processes was also postulated by Pellionisz and Llinas (1979). The adequate functioning of sensorimotor loops requires some kind of consistency in sensory and motor signal coding; this consistency is provided by the definition of metrical tensors and other derived metrical operators.

The question arises whether these geometric operators are rigidly determined—by some genetic mechanisms, for instance—or are subject to adaptive changes, in order to keep the internal representations of space consistent with the physical space.

This question was first addressed by Rock

(1966), who found experimental evidence of perceptual adaptation to optical minification. Sensorimotor adaptations have been shown to occur also when people or animals are continuously exposed to a modified visual environment. Since the original experiments of Helmholtz (1866), who used laterally displacing prisms, and of Stratton (1897), who wore up-down inverting spectacles for several days, many authors have obtained significant visuomotor adaptation with human subjects or animals (Gonshor and Melvill Jones, 1973; Gauthier and Robinson, 1975; Miles and Fuller, 1974). For instance, vestibulo-ocular reflex (VOR) adaptation was initially interpreted in terms of gain and phase modifications, due to retinal error signals; but since such changes have been proved to be plane-specific (Berthoz *et al.*, 1981) and elicited by pure mental effort in darkness (Melvill Jones *et al.*, 1984), more complex mechanisms of adaptation have been considered (Robinson, 1982; Pellionisz, 1985; Droulez *et al.*, 1985).

The present experiment was aimed at finding evidence of adaptive mechanisms acting on the metrical operators involved in perception as well as in sensorimotor coordination. In this study, we used distorting lenses, which induce anisotropic optical deformation of the subject's visual field. Instead of over-all modification such as inversion or magnification, these lenses produce selective vertical lengthening, thus leaving the horizontal direction as reference for the measurement of vertical changes. As plane-specificity of VOR adaptation has been demonstrated in previous studies, the modifications induced in visual processes by distorting lenses are expected to be direction-specific and not reducible to a simple parametric gain control.

## METHODS

### Lenses

We used three separate pairs of cylindrical lenses, with the concave side facing the eye. The

total optical power of each lens was null and the alteration of the retinal image was due only to refraction phenomena (Fig. 1). The axes of the cylindrical faces of a lens were in the horizontal plane of the eye, so that there was little or no disturbance of the visual input in the horizontal direction; in particular, changes in binocular convergence were very slight, due only to the thickness of the lenses. Because of the curvature of the lenses, the vertical disturbance was a magnification of 5, 8 or 26%, which varied weakly according to the distance of the object seen, while the ratio of vertical lengthening to horizontal lengthening was respectively 5, 8 and 25%.

Because of the selective lengthening in the vertical direction, oblique lines appeared slightly rotated towards the vertical, and any rotation of an object relative to the observer, around the visual axis, induced a perceived deformation of the object. Moreover the vertical VOR had to adapt to maintain the retinal stabilization of images during pitch head movements.

The 25% lenses were fixed on masking goggles which restricted the visual field to that seen through the lenses. This restriction of the visual field, to about  $50^\circ$  in vertical and  $70^\circ$  in horizontal, was the major source of constraint during the experiment, though the subjects quickly became used to making many more head movements than usual. The other lenses were worn like ordinary spectacles.

### Subjects

The 12 subjects (6 women, 6 men) were 20–26 years old, had normal uncorrected vision, and were right-handed. All of them were naive subjects, and they were paid for taking part in the experiment.

They were asked to wear the lenses continuously for the entire experimental period (1, 3, 4, 7 or 9 days). They were tested before the experiment ("control tests") and when wearing

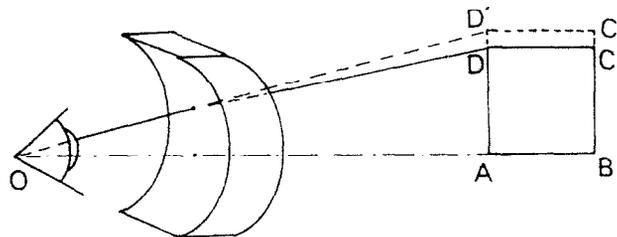


Fig. 1. Optical effect of the lenses. Both faces of each lens are horizontal cylinders with the concavity facing the eye. The square ABCD viewed through these lenses by observer O appeared as a vertical rectangle ABC'D'.

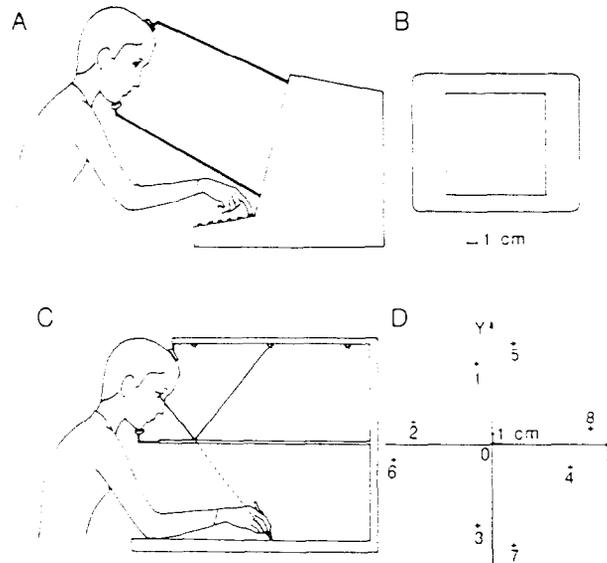


Fig. 2. Experimental set-up. (A) Perceived-square test. The subject's head was held still by a chin-rest. A black tunnel blocked peripheral vision. The subject looked at rectangles displayed on the screen and pressed a key according to his perception. (B) Example of a displayed rectangle. (C) Pointing test. The subject looked at targets through a horizontal mirror and pointed with a pen to the target images on the plane of the digitizing tablet. (D) Positions of the 8 targets around the central point O.

the lenses ("adaptation tests") as well as after taking them off ("post-adaptation tests"). All subjects were encouraged to live normally while wearing the lenses.

#### Experiments

Two experiments were performed in order to evaluate the influence of two parameters: the intensity of the distorting effect and the duration of exposure.

*Experiment A.* One subject wore the 8% lenses for 9 days, two subjects, the 8% lenses for 7 days, and one subject, the 5% lenses for 7 days. Before, during, and after the period of wearing the lenses, they were submitted daily to two tests: the "perceived-square test" and the "perceived-orthogonality test", which characterized the perceived lengthening effect of the lens and the subject's perceptual adaptation.

*Experiment B.* Four subjects wore the 25% lenses for 1 day, one subject for 3 days, one subject for 4 days, and one subject for 7 days. All of them were tested once or twice a day to assess their visuomotor adaptation (the pointing test) as well as their perceptual adaptation (the perceived-square test).

#### Perceived-square test

*Apparatus.* Luminous rectangles, with edges either vertical or horizontal, were displayed 57 cm in front of the subject. The subject's head

was held still by a chin-rest and surrounded by a black tunnel in order to block out lateral vision [Fig. 2 (A and B)].

*Design.* Rectangles were generated by computer on a Hewlett Packard Graphics Terminal. Their height/width ratio (HWR) ranged between 0.75 and 1.25 but their area was constant:  $0.01 \text{ m}^2$ . For each trial, the following convergent procedure was used:

- Presentation of a first rectangle with a randomly chosen HWR.
- Depending on the subject's response, the HWR was incremented or decremented by one "step", which was initially set to 0.1.
- After two opposite responses, the step was divided by 2.

The test ended when the step became smaller than the resolution of the display (0.3 mm).

*Procedure.* In this forced-choice test, for each rectangle the subject was asked to indicate whether he perceived it as horizontal (height < width) or vertical (width < height). A session consisted of 40 trials, each one establishing the HWR of what seemed a square to the subject. The means and standard deviations of the HWR were computed for each session.

#### Perceived-orthogonality test

The experimental set-up of this test was the same as for the perceived-square test, except

that the subjects were presented with two oblique lines on the screen. The two lines intersected at their middle-point and lied symmetrically about an horizontal axis located in the plane of the screen. Each line was 5.8 cm long. The subjects could change the angle formed by these two lines, and were instructed to adjust this angle to perfect orthogonality. This was repeated 20 times, starting from various initial angles. The main results of this test are the mean and the standard deviation of the final angle, corresponding to what the subject considers to be a right angle.

#### Pointing test

*Apparatus.* The subject was seated at arm's length from a horizontal digitizing tablet, or "pointing surface" [Fig. 2(C)]. The visual display consisted of an array of 9 targets numbered from 0 to 8 [Fig. 2(D)]. This array was placed under the top side of a box: the subject could see the targets in a mirror fixed horizontally in the box, at an equal distance from the top side and the digitizing tablet. Therefore the image of the pattern of targets was located on the pointing surface. The subject required to point to them under the mirror and on the surface with a 15-cm long electronic pen. He was positioned in a chin-rest, so that the central point appeared to him to be straight ahead of his nose and was about 50 cm from his eyes.

The coordinates of the 8 targets and their distances from the origin, target 0, are reported in Table 1.

*Design.* The horizontal and vertical ( $X$  and  $Y$ ) resolution of the digitizing tablet (Calcomp 600) was 1/100 in. The pencil's position was sampled every 10 msec and stored on-line by the computer. The starting position was checked, and an acoustic signal was generated when the absolute error on starting (position 0) was less than 1 mm. The target point was then randomly chosen between 1 and 8 and displayed by the computer.

*Procedure.* A session consisted in 15 pointings at each of the 8 targets. Before each pointing the

subject had to come back to target 0, helped by the acoustic feedback. When target 0 was found, the subject was told a randomly chosen number (read by the experimenter on the computer terminal) between 1 and 8, and had to point the corresponding target.

The  $X$  and  $Y$  coordinates of the pencil were sampled by the computer after the arm movement. For each target, mean values and standard deviations were calculated. The mean  $Y$  coordinates of points 1, 3, 5 and 7 and mean  $X$  coordinates of points 2, 4, 6 and 8 [see Fig. 2(D)] were used to compute two averaged height/width ratios (HWR)

$$\text{HWR1} = (Y1 - Y3)/(X2 - X4)$$

$$\text{HWR2} = (Y5 - Y7)/(X6 - X8).$$

The changes in HWR1 (or HWR2) reflect modifications of vertical with respect to horizontal pointing performances for small (or large, respectively) arm movements. Indeed, HWR1 and HWR2 are normalized in the following sense. They are both equal to the amplitude (projected on a vertical axis) or vertical movements, divided by the amplitude (projected on an horizontal axis) of horizontal movements. The ideal subject, who would point exactly where he sees the image of each target, should exhibit an increase of 25% of HWR1, as well as HWR2, when he first puts the 25% lenses on.

## RESULTS

#### Perceived-square test

Eleven subjects took this test before, during, and after adaptation periods of various durations (1, 3, 4, 7 or 9 days) to the 5, 8 or 25% lenses. The two experimental parameters are reported in Table 2, rows 2 and 3.

The control tests performed before the subjects had worn the lenses revealed the good reliability of this perceptual test and allowed the determination of a control value of the HWR (height/width ratio) of the subjective square (see Table 2, row 4). The intra subject variation from day to day was commonly less than 2% while

Table 1. Pointing test

Target	1	2	3	4	5	6	7	8
$X$	-1.5	-8.0	-1.5	8.0	2.2	-10.0	2.2	10.0
$Y$	8.0	2.2	-8.0	-2.2	10.0	-1.5	-10.0	1.5
$d$	8.1	8.3	8.1	8.3	10.2	10.1	10.2	10.1

$X$  and  $Y$  coordinates of the 8 targets on the pointing surface [target 0 is the origin, see Fig. 2(D)] and the distances  $d$  of these targets from target 0.  $X$ ,  $Y$  and  $d$  are in cm.

Table 2. Perceived-square test

1 Subject	2 Lense effect (%)	3 Exposure duration (days)	4 Contrôle ( $\pm$ SD)	5 Initial decrease (%)	6 Final increase (%)	7 Adaptation % (significant)	8 After effect (%)	9 Adaptation rate (%) per day)
E.V.	25	1	1.008 ( $\pm$ 0.015)	25.2	28.2	-0.7 (NS)	0.9 (NS)	0
A.L.	25	1	0.968 ( $\pm$ 0.035)	31.0	27.9	5.5 ( $P < 0.01$ )	2.2 ( $P = 0.02$ )	3.8
C.L.	25	1	0.979 ( $\pm$ 0.012)	27.1	26.3	3.1 ( $P < 0.01$ )	2.8 ( $P < 0.01$ )	3.0
I.D.	25	1	1.060 ( $\pm$ 0.035)	23.0	24.1	0 (NS)	1.0 (NS)	0
X.M.	25	3	0.968 ( $\pm$ 0.012)	23.5	25.8	0.20 (NS)	3.7 ( $P < 0.01$ )	0.7
L.B.	25	4	1.054 ( $\pm$ 0.020)	18.6	22.2	4.6 ( $P < 0.01$ )	6.0 ( $P < 0.01$ )	1.3
C.C.	25	7	0.958 ( $\pm$ 0.010)	22.8	24.5	4.5 ( $P < 0.01$ )	6.9 ( $P < 0.01$ )	0.8
A.B.	8	7	0.920 ( $\pm$ 0.015)	8.7	4.9	6.8 ( $P < 0.01$ )	3.0 ( $P < 0.01$ )	0.7
G.C.	5	7	0.940 ( $\pm$ 0.015)	6.1	6.6	2.9 ( $P < 0.01$ )	3.4 ( $P < 0.01$ )	0.5
C.R.	8	7	1.025 ( $\pm$ 0.015)	8	8.3	7.3 ( $P < 0.01$ )	7.6 ( $P < 0.01$ )	1.1
T.J.	8	9	0.970 ( $\pm$ 0.015)	9.5	6.2	4.0 ( $P < 0.01$ )	1.0 ( $P < 0.01$ )	0.3

the standard deviation for a given session ranged from 1 to 3.5%. Mean values of HWR differed significantly according to the subject (0.920 to 1.060; mean value, 0.984).

As soon as the subjects put the lenses on, a marked decrease, relative to the control value, occurred in the recorded HWR. This initial decrease generally matches quite well the optical effect of the lenses, determined by a calculation of the refraction. This shows that subjects' responses depended on the modified retinal images of the rectangles and not on contextual or cognitive information. Similarly, after removal of the lenses, an immediate increase of the HWR, roughly equal to the initial decrease, was observed. These two effects, which reflect the optical perturbation, are reported in Table 2, rows 5 and 6. The mean initial decrease and final increase observed for the 7 subjects who wore 25% lenses were 24.5 and 25.5% respectively. The adaptation (Table 2, row 7) was measured from the difference between the mean HWR recorded just before the removal of the lenses and on the first few minutes after putting them on. As these two values were obtained in the same experimental conditions, the difference between them reflects a modification in the perceptual visual process.

Short experiments (8 hr) were performed on four subjects. Only two of them exhibited significant adaptation.

Long-term adaptation was studied on 7 subjects (Figs 3 and 4). While wearing lenses, all the subjects' responses tended to return slowly to the control values. In some cases, this adaptation was already noticeable after 24 hr of continuous wearing. The final adaptation measures (Table 2, row 7) were all significant, except for subject X.M.

The aftereffect, measured from the difference

between the control value and the HWR value observed in the first test performed just after removal of the lenses, is a second quantification of the change in the perceptual process (Table 2, row 8). The two adapted subjects in short experiment also exhibited a significant aftereffect. All the subjects in the long experiment displayed a significant aftereffect measure.

Divided by the number of exposure days, the mean of adaptation and aftereffect measures can be considered an estimation of the adaptation rate for each subject (Table 2, row 9); the values ranged from 0 to 3.8% per day (mean 1.1% per day).

The general conclusion we draw from this experiment is that the perceptual adaptation is highly variable between subjects, particularly during short exposure. In long-term experiments, a slightly higher rate of adaptation was observed with strong lenses (mean 0.93% per day) than with weak lenses (mean 0.65% per day), but because of inter subject variability this difference is not statistically significant.

#### *Perceived-orthogonality test*

Two subjects (A.B. and C.R.) took this test before, during, and after a period of long-term adaptation (7 days) to 8% lenses. The standard deviation for a given session ranged from 1 to 1.7%, while the intra subject variation from day to day, for the control tests, was less than 0.7%. The control values for subjects A.B. and C.R. were respectively 93.1 and 90.5°. The adaptation profile was roughly similar to what we observed in the perceived-square test (Fig. 3, subjects A.B. and C.R.).

In order to compare the results of these two perceptual tests, the apparent widening of angles had to be expressed in terms of lengthening effect. When a subject first put the lenses

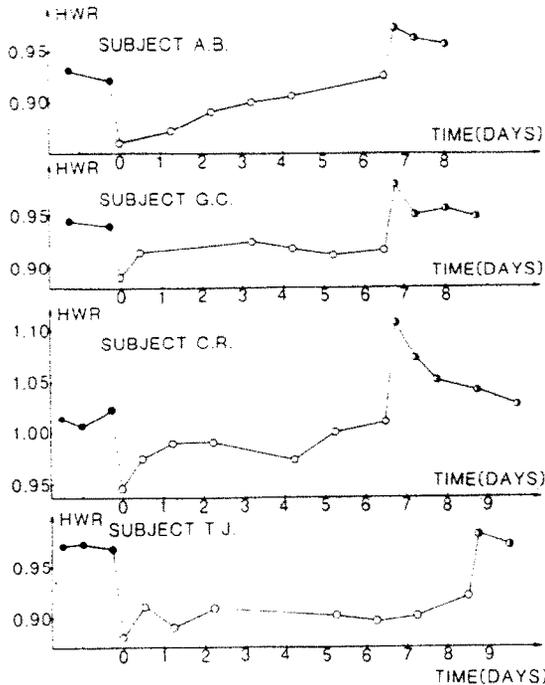


Fig. 3. Perceived-square test. Collected results for the subjects wearing the 8% lenses (A.B., C.R. and T.J.) and the 5% lenses (G.C.). Abscissa: time of exposure (days), starting at the beginning of lens wear. Ordinate: the mean height/width ratio (HWR) of a rectangle perceived as a square by the subjects, before (solid circles), during (open circles), and after (half-solid circles) lens wear.

on, he adjusted the test lines to an angle  $x$ , which seemed to him to be equal to the control value  $x'$ . A simple calculation leads to the measure  $g$  of the lengthening effect of the lenses

$$g = \frac{\tan(x'/2) - \tan(x/2)}{\tan(x/2)}$$

If  $g$  depended only on the optical effect of the lenses, it should match the value 8%. According to the formula, we could calculate the initial decrease and final increase for subject A.B.: 9.3 and 5.0%, respectively, and for subject C.R.: 3.3 and 5.2%. Three of these four values are much weaker than the optical effect of the lenses (8%).

The time-course of the adaptation was also faster (1 or 2 days) than with the perceived-square test. Subject C.R. adapted well as shown by an adaptation of 2.3% and an after effect of 4.1%, with respect to the control values. On the second day, subject A.B. reached an adaptation of 6.1% which did not change later. On the other hand his aftereffect was only 1.4%.

Statistical comparison of the results of the two perceptual tests showed a strong positive correlation ( $r = 0.79$  and  $r = 0.86$ ) for both subjects.

Pointing test

Three subjects performed this visuomanual coordination test; all of them wore 25% lenses, but for various periods: 3, 4 or 7 days. As in the perceived-square test, their responses were measured before, during, and after lens wear.

Figure 6 shows the HWR1 and HWR2, and their mean. HWR2, which corresponds to large arm movements, is systematically higher than HWR1. The mean ratio HWR2/HWR1 averaged for all sessions of the three subjects was 1.066 (standard deviation 0.06).

These adaptation curves can be compared to the perceived-square test results of the same subjects (Fig. 4). In Fig. 6, curves A and B, subjects X.M. and L.B. exhibit a complex adaptation process, with rather small initial increases (11.5 and 14%) and after-removal decreases (4.2 and 11%). Subject L.B. had not returned to the initial values by even 3 days after removal of the lenses. Therefore a control value could not be

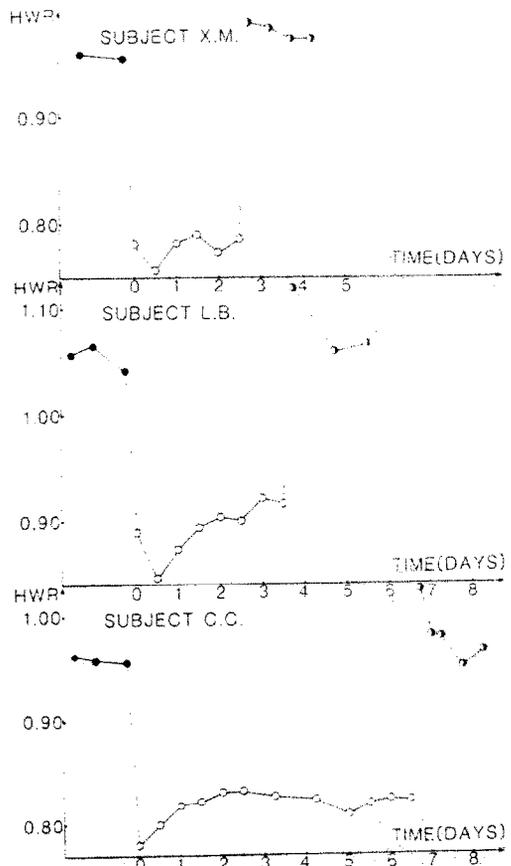


Fig. 4. Perceived-square test. Collected results for the subjects wearing the 25% lenses for 3 days (X.M.), 4 days (L.B.), or 7 days (C.C.). Abscissa: time of exposure (days), starting at the beginning of lens wear. Ordinate: mean HWR before (solid circles), during (open circles), and after (half-solid circles) lens wear.

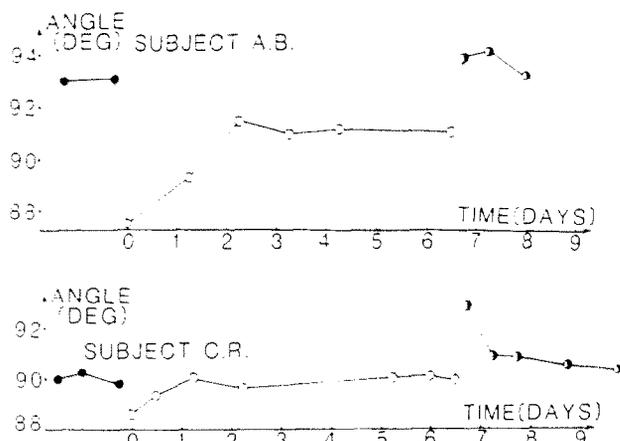


Fig. 5. Perceived-orthogonality test. The two subjects (A.B. and C.R.) wore the 8% lenses for 7 days. Abscissa: time of exposure (days), starting at the beginning of lens wear. Ordinate: mean angle (in degrees) between two oblique lines which were perceived as orthogonal by the subjects, before (solid circles), during (open circles), and after (half-solid circles) lens wear.

defined clearly and visuomanual adaptation was not demonstrated for these two subjects.

However, one subject (C.C., curve C in Fig. 7) exhibited a clear adaptation profile:

initial increase	26.9%
final decrease	28.6%
adaptation measure	6.0%

aftereffect measure	7.5%
mean adaptation rate	0.96% per day.

The horizontal (*X*) and vertical (*Y*) coordinates of each of the eight targets in the pointing test were plotted against time for subject C.C. [Fig. 7(A) and (D)]. There was no significant change on the *X* coordinates of all points, nor

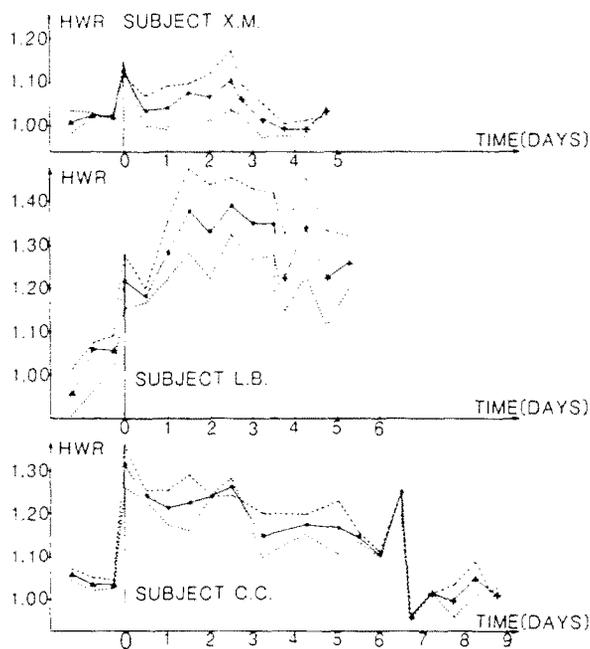


Fig. 6. Open-loop pointing test. Collected results for the 3 subjects who wore the 25% lenses for 3 days (X.M.), 4 days (L.B.), or 7 days (C.C.). Abscissa: time of exposure (days), starting at the beginning of lens wear. Ordinate: the averaged HWR1, HWR2, and their mean computed from the coordinates of the pen position at the end of the pointing movement (see text for explanation). HWR1 (small dots) was calculated for the 4 targets close to the central point. HWR2 (broken line) was calculated for the 4 targets far from the central point. The mean value of HWR1 and HWR2 is shown by the continuous line. The two light vertical lines indicate the beginning and the end of lens wear.

on the  $Y$  coordinates of the four points near the horizontal axis (2, 4, 6 and 8). The main changes were observed for the four points distant from the horizontal axis, namely targets 1, 5, 3 and 7. Adaptation and aftereffect appear significantly on these four individual traces.

The  $X$  and  $Y$  lateral deviations [Fig. 7(B) and (E)] were obtained by averaging the difference between  $X$  (or  $Y$ ) signed coordinates of the recorded point and the actual position of the corresponding target. Similarly the  $X$  and  $Y$  spread [Fig. 7(C) and (F)] were calculated by averaging the difference between  $X$  (or  $Y$ ) unsigned coordinates.

During the experiment no significant change was observed for the lateral deviations along either axis. On the other hand, a mean spread of 1.31 cm on the  $X$  axis and 1.53 cm on the  $Y$  axis was found even in the control experiments. As soon as the subject wore lenses, the  $Y$ -axis spread rose to 3.66 cm; it slightly decreased to 2.64 cm on the last two days of lens wear.

#### Verbal reports

When they first put the lenses on, all the subjects experienced a marked subjective length-

ening of objects and faces in the vertical direction. They also reported surface distortions (especially with the 25% lenses on): a large flat surface appeared concave. Head movements induced an apparent motion of the peripheral visual field, and a feeling of slight loss of equilibrium.

These subjective impressions did not prevent the subjects having a normal visuomotor coordination. The only difficulty came from the reduction of the visual field in the case of the 25% lenses; for instance, while walking, subjects had to make voluntary head movements in order to look at their feet. Except for this constraint all the subjects were relatively comfortable with the lenses in everyday life.

After 1 day, the subjects were still aware of the lengthening effect and of the distortions but claimed that these effects did not bother them. When the glasses had just been removed, the opposite effects were experienced, especially by subjects who had worn the lenses for more than 1 day. Contrary to Gauthier and Robinson's experiment (1975), none of the subjects experienced nausea or vertigo while or after wearing the lenses.

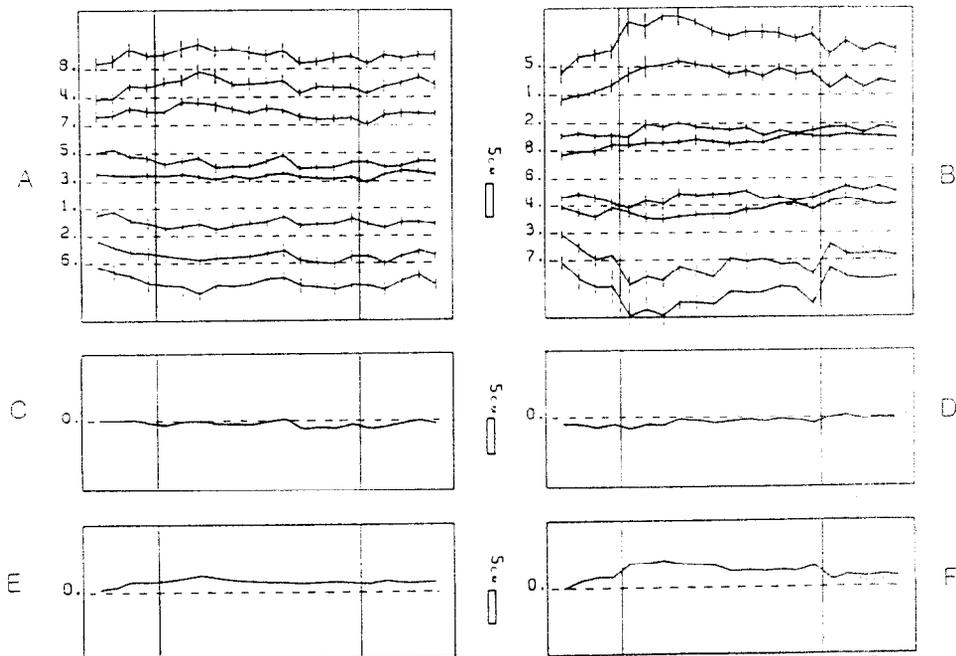


Fig. 7. Data processing of the pointing test for one subject (C.C.). Abscissa, for all traces: time of exposure. The two light vertical lines indicate the beginning and the end of lens wear. The upper traces represent respectively the horizontal  $X$  (A) and the vertical  $Y$  (B) positions of the pen for the 8 individual targets with standard deviations (vertical bars). The actual coordinates of the targets are indicated by broken lines. The middle traces represent respectively the averaged horizontal (C) and vertical (D) position shifts with respect to the actual target positions. The lower traces represent respectively the averaged horizontal (E) and vertical (F) spreads with respect to the actual target positions. See text for the calculation of averaged shift and spread.

## DISCUSSION

Our results indicate clearly that:

(1) The subjects could compare lengths precisely in the horizontal and the vertical directions. The intra subject variability in this perceptual task was about 2%. Subjective judgements of orthogonality were also highly reliable.

(2) These metrical estimations underwent long-term plastic adaptive changes. The rate of adaptation was, however, relatively slow (less than 1% per day for long-term exposure) and roughly independent of the initial degree of optical distortion.

(3) The variability in response in a visuomanual task such as pointing in open-loop conditions was about one order of magnitude higher than in a purely perceptual task.

(4) Despite this variability, a slow process of adaptation of visuomanual coordination was also shown.

(5) For one subject there was a strong negative correlation ( $r = -0.92$ ) between perceptual and visuomanual adaptation.

Our results can be interpreted as the consequences of slow adaptive changes in a metrical operator, such as a metrical tensor (Pellionisz and Llinas, 1979) or a Riemann connection (Droulez, 1985).

It should be pointed out that subjects were immediately aware of the optical effect of the lenses: they reported that they perceived familiar objects and faces as lengthened vertically. Therefore, we cannot exclude a purely cognitive process, that is, systematic correction by subjects for the optical effect. However, the relative slowness of the response changes does not support this hypothesis. Moreover, the existence of a marked aftereffect is difficult to explain in terms of a purely cognitive correction.

The relative weakness of changes in judgements of orthogonality during exposure to optical distortion may be due to the display device that we used. As it was a digital display the lines were constructed from series of adjacent dots which were not exactly in a straight line except when the orientation was 0, 45 or 90° with respect to the horizontal. Subjects might detect such misalignments and accordingly adjust their judgements of orthogonality towards physically orthogonal angles. Despite this possible technical bias, the optical effect of the lenses was clearly seen on the two subjects tested. There was also good statistical correlation between

judgement of orthogonality and judgement of relative lengths.

Adaptation of metrical judgements was investigated by Rock (1966), who demonstrated rapid adaptation to a reducing mirror and a miniature world, using the subjective comparison between a test line and a standard memorized line. The relatively fast adaptation he reported (after 30 min of exposure), as opposed to our slow adaptive process, may be due to the differences in experimental methods. In Rock's experiment, the test line and the standard line were presented in different contexts and at different periods. Moreover the difference in length judgement may be due to a change in depth estimation (Wallach and Frey, 1972). In our experiment, subject responses relied on simultaneously presented visual stimuli. Thus any effects of context or depth estimation would have been cancelled.

Visuomotor adaptations have been shown to occur when subjects or animals are exposed to continuous optical deformations. Modifications of the vestibulo-ocular reflexes have been studied with left-right inverting goggles (Gonshor and Melvill Jones, 1973; Melvill Jones *et al.*, 1984), and with magnifying lenses (Gauthier and Robinson, 1975; Miles and Fuller, 1974; Istl-Lenz *et al.*, 1985). Visuomanual adaptations have also been reported during exposure to distorting lenses (Mandelbrojt *et al.*, 1984). For the same wearing period, those authors in some cases found higher rates of adaptation than those exhibited in our experiment. This may be attributed to the differences between the optical devices: the direction specificity of visuomotor adaptation to our lenses might imply more complex processes than those yielded by isotropic transformations of the visual field. However, the discrepancies are probably mainly related to the training methods: fast sensorimotor adaptations are generally obtained by intensive training of subjects to the specific task performed in closed-loop conditions; consequently, the adaptive changes are more or less specific to the test and do not necessarily involve a fundamental reorganization of sensory and motor maps.

It should also be pointed out that fast sensorimotor changes can be achieved by new motor programs, learned during the intensive training sessions. On the other hand, "natural" conditions of training yield a relatively slow rate of adaptation, with perceptual and sensorimotor changes in a close relationship.

While the goal of sensorimotor adaption is clear, that of the perceptual changes were observed is less evident. Indeed, that there is a slight natural anisotropy of the perceptual space, was demonstrated long ago (Zusne, 1970): vertical lines appear a little longer than horizontal ones of the same physical length.

More generally, one might wonder what the constraints are which force the central nervous system to develop metrical operators on internal representations of space, which mimic its physical metrical properties: why a straight line, a circle, a plane must be perceived as such in conformity with their geometrical characteristics. We advance the hypothesis that the main constraint is produced by the perception of motion, and particularly of self motion. More precisely, we assume that the central nervous system modifies its metrical operators so that the movements of the observer leave the perceived metrical properties of the visual environment unchanged.

With our lenses for instance, before adaptation, rotations of the head around the horizontal axis of gaze produce an important distortion of the visual scene. Then the perceptual changes tend to restore the metrical invariance of the objects, or in other words, to restore the subject/object independence.

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#### REFERENCES

- Bach-y-Rita P. (1972) *Brain Mechanisms in Sensory Substitution*. Academic Press, New York.
- Berthoz A., Melvill-Jones G. and Bégue A. E. (1981) Differential visual adaptation of vertical canal dependent vestibulo-ocular reflexes. *Expl Brain Res.* **44**, 19–26.
- Droulez J. (1985) Neurosensory processing of moving images. *Biol. Cybernet.* In press.
- Droulez J., Berthoz A. and Vidal P. P. (1985) Use and limits of visual vestibular interaction in the control of posture. In *Vestibular and Visual Control on Posture and Locomotion Equilibrium* (Edited by Igarashi and Black), pp. 14–21. Karger, Basel.
- Gauthier G. M. and Robinson D. A. (1975) Adaptation of the human vestibulo-ocular reflex to magnifying lenses. *Brain Res.* **92**, 331–335.
- Gibson J. J. (1966) *The Senses Considered as Perceptual Systems*. George Allen & Unwin Ltd.
- Gonshor A. and Melvill Jones G. (1973) Changes of human vestibulo-ocular response by vision reversal during head rotation. *J. Physiol., Lond.* **234**, pp. 102–103.
- Helmholtz H. von (1866) *Handbuch der physiologischen Optik*. Vos, Leipzig.
- Isti-Lenz Y., Hydén D. and Scharz D. W. F. (1985) Response of the human vestibulo-ocular reflex following long term  $2 \times$  magnified visual input. *Expl Brain Res.* **57**, 448–455.
- Jeannerod M. (1975) Déficit visuel persistant chez les aveugles nés: données cliniques et expérimentales. *Année psychol.* **75**, 169–196.
- Johansson G. (1977) Spatial constancy and motion in visual perception. In *Stability and Constancy in Visual Perception* (Edited by Epstein W.), pp. 375–419.
- Johansson G. (1978) About the geometry underlying spontaneous visual decoding of the optical message. In *Formal Theories of Visual Perception* (Edited by Leuvenberg E. L. and Buffart H. F. J.), pp. 265–276. Wiley, New York.
- Longuet-Higgins H. C. and Prazdny K. (1980) The interpretation of a moving retinal image. *Proc. R. Soc. Lond. B* **208**, 385–397.
- Mandelbrojt P., Gauthier G. M., Vercher J. L., Ouaknine M. and Obrecht G. (1984) Ensemble expérimental pour l'étude des propriétés adaptatives du système visuo-manuel chez le sujet nouvellement équipé de corrections optiques. *J. Fr. Ophthal.* **7**, 157–165.
- Melvill Jones G., Guitton D., Berthoz A. and Volle M. (1983) Rapid effects of vision reversal on head eye coordination. *Soc. Neurosci. Abstr.* **9**, 867.
- Melvill Jones G., Berthoz A. and Segal B. (1984) Adaptive modification of the vestibulo-ocular reflex by mental effort in darkness. *Expl Brain Res.* **56**, 149–153.
- Miles F. A. and Fuller J. H. (1974) Adaptive plasticity in the vestibulo-ocular responses of the Rhesus monkey. *Brain Res.* **80**, 512–516.
- Pellionisz A. (1985) Tensorial aspects of the multi-dimensional approach to the vestibulo-oculomotor reflex and gaze. Reviews of oculomotor research. In *Adaptive Mechanisms in Gaze Control* (Edited by Berthoz A. and Melvill Jones G.) Elsevier, Amsterdam.
- Pellionisz A. and Llinas R. (1979) Brain modeling by tensor network theory and computer simulation. The cerebellum: distributed processor for predictive coordination. *Neuroscience* **4**, 323–348.
- Piaget J. (1975) *Les mécanismes perceptifs*. Presses Univ. de France, Paris.
- Robinson D. A. (1982) The use of matrices in analyzing the three-dimensional behavior of the vestibulo-ocular reflex. *Biol. Cybernet.* **46**, 53–66.
- Rock I. (1966) *The Nature of Perceptual Adaptation*, pp. 145–175. Basic Books, New York.
- Stratton G. (1897) Upright vision and the retinal image. *Psychol. Rev.* **4**, 182–187.
- Todd J. T. (1984) The perception of three-dimensional structure from rigid and non rigid motion. *Percept. Psychophys.* **36**, 97–103.
- Ullman S. (1979) *The Interpretation of Visual Motion*. MIT Press, Cambridge, Mass.
- Wagner M. (1985) The metric of visual space. *Percept. Psychophys.* **38**, 483–495.
- Wallach H. and Frey K. J. (1972) Adaptation in distance perception based on oculomotor cues. *Percept. Psychophys.* **II** (1B), 77–83.
- Wallach H. and O'Connell D. N. (1953) The kinetic depth effect. *J. exp. Psychol.* **45**, 205–217.
- Zusne L. (1970) *Visual Perception of Form*. Academic Press, New York.