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RESEARCH ARTICLE

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Long-term adaptation to prism-induced inversion of the retinal images

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Abstract For 1 week, healthy human participants (n=7) were devoid of normal vision by exposure to prism lenses that optically rotated their perceived world around the line of sight by 180°. Adaptation to such prisms involved sustained and vigorous practice of the ability to redirect the unadapted efferent motor command; because prior to all visually guided movements, the to-be-executed efferent command was based on incorrect (prismatically reversed) spatial information. The time course of this sort of adaptation was systematically explored in Cooper-Shepard mental rotation (MR) tests and in naturalistic motor-tasks for the purpose of investigating whether mental rotations of the direction of the intended movement share common aspects with the process of MR. A control group (n=7) intermittently exposed to the distorted spatial organization of the central visual field was studied in parallel. The main results were as follows: (a) the MR reaction times (RTs) day 1 with prisms appeared to be very similar to the normal RTs (day 1, no-prisms) with the one exception that subjects now responded within a prism (rotated) frame of spatial reference rather than within the environmentally upright. The visuomotor performance became grossly irregular and dysmetric. (b) The majority of the visuomotor adaptation functions began to level off on the 3rd day. (c) The increases in natural motor proficiency were accompanied by a systematic and noticeable decrease in magnitude of the MR Y-intercept obtained from the linear regression line calculated between each subject's RT and the various stimulus angles. MR slopes were stable through days 1–7 for both the experimental and control group. An increased correlation between rotational stimulus angle and RT suggested that the MR function also became progressively more tightly coupled to the stimulus angles. (d) Postadaptation measures of performance indicated the occurrence of selective and minimal adaptation in the natural motor tasks only. It is suggested that these results reflect an improved attentional (strategic) ability to replace incorrect (error producing) control signals with correct (error reducing) control signals. As a result, perceptual-motor start-up processes directly related to spatial coding and to the planning, initiation and correction of the intended direction of motor-or-mental movement improved while the subprocess ("stage") concerned with transformations of such movements remained unchanged. Visuomotor adaptation to inverting prisms engages, and thereby stimulates, a cortical system also invoked in the preparatory process of MR.

Keywords Attention · Experience dependent plasticity · Mental rotation · Motor imagery · Posterior parietal lobule · Sensorimotor adaptation

Introduction

About 100 years ago, Stratton conducted studies with a prism lens that optically rotated the perceived world around the line of sight by 180° (Stratton 1896, 1897). Spatial distortion by such a lens has many dramatic effects on central higher-order visual-motor control loops (cf. Hein and Held 1962; Held and Freedman

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1963; Kohler 1964; Mikaelian and Held 1964; Harris 1965; Redding and Wallace 1988; Clower et al. 1996; Imamura et al. 1996; Redding and Wallace 1996; Rossetti et al. 1998; Kurata and Hoshi 1999; Linden et al. 1999; Sekiyama et al. 2000; Rossetti et al. 1996; Farne et al. 2001; Tilikete et al. 2001; Rode et al. 2001). A stationary target to which one is about to move, for example, is not seen in its veridical position. Prior to movement, the to-be-executed efferent command is therefore based on incorrect spatial information. When movement of the hand begins, the combination of visual and proprioceptive feedback becomes more crucial than is normally the case for in-course guidance, in order to modify the initially incorrect efferent command. Perceptual-motor adaptation to the prisms involves, among other things, the comparison and mental rotation (MR) of the reversed visual information coded within a visual map and the proprioceptive information coded within normal (e.g., somatosensory and auditory) maps.

What we hope to consider here is how this type of visuomotor adaptation manifests itself following long-term prism wear and specifically if mental rotations of the direction of the intended movement share common aspects with the process of MR of alphanumerical characters. We believe this may be true since it has often been suggested that some types of visual MR are covert simulations of motor events in which the simulated action is imagined before its execution (Georgopoulos et al. 1986; Schwartz et al. 1988; Finke 1989; Pellizzer and Georgopoulos 1993; Bonda et al. 1995; Georgopoulos and Pellizzer 1995; Georgopoulos et al. 1995; Parsons et al. 1995; Pellizzer et al. 1995; Wexler et al. 1998; Ganis et al. 2000; Richter et al. 2000).

Specifically, in protocol 1, which was the first of four tests, Cooper-Shepard MRs (Cooper and Shepard 1973) were explored under the hypothesis that the associated RTs probe operations central to preparation of movements. Actual movements were studied in parallel, in three visuomotor tests (protocols 2–4) and in naturalistic tasks requiring differential degrees of limb and muscle involvement. In protocol 2 we tested the effects of the prisms on the performance of subjects tracing narrow paths and examined specifically how adaptation influenced this ability. In protocol 3 we tested the effects of the prisms on the coordination between eye position and synergy of the arm throw in a dart throwing task, and asked how adaptation influenced this particular skill. The task employed in protocol 4 aimed at testing the effects of the prisms on the ability to ambulate forward and sideways through a predetermined obstacle course, and in particular examined how adaptation influenced the coordination between eye position and head position. Motor performance and MR performance were thus tested in the same individuals during successive days of the experiment, thereby allowing direct observation of the degree to which motor learning had an impact on the MR performance.

Materials and methods

This experiment consisted of four tests (protocols 1–4). In this section we start out by describing methodological aspects common to all four protocols. Below we outline, in subsections, the specific aspects associated with protocols 1–4.

Volunteers

Seven naive male volunteers, with a mean age of 25 years (SD ±2.3 years), participated in the experimental group. Seven additional inexperienced male volunteers, with a mean age of 27 years (SD ±4.9 years), constituted the control group. All participants were unpracticed. Each subject who obtained a monetary reward upon completion of the study gave informed consent according to ethics committee guidelines. The local ethics committee approved the study.

Prisms

Binocular prism glasses (Takei Kiki Kogyou Co., Japan) inverted the visual field (i.e., rotated the perceived world around the line of sight by 180°). Distance between the centers of the two prisms was 60 mm. The total weight was approximately 310 g. Binocular viewing with the prism glasses yielded a field of view corresponding to ~55° horizontally and ~32° vertically. The peripheral visual field was fully occluded.

Visuomotor adaptation

The participants in the experimental group were exposed to 7 days of prism-induced inversion of the retinal images. Ambulation and significant head movements were encouraged during engagement in normal activities (e.g., attending lectures) when the subject was not taking part in the daily tests. Complete control of the subjects' compliance with the instruction provided not to open the eyes while without prisms was not possible due to experimental procedures involving overnight housing and assistants only being physically present only from the early morning until the evening (not present at night).

Experimental design

The time course of adaptation occurring in response to the prolonged exposure to the prisms was systematically explored once a day by measuring error rates and the time it took to: (1) carry out a Cooper-Shepard MR task (Cooper and Shepard 1973); (2) trace a templated path; (3), throw darts; and (4) ambulate forward or (5) sideways through a narrow obstacle course. The order of these tests was randomized within subjects. It took 30 min to complete all of the protocols for any given participant and for any day of testing. Seven control subjects performed identical sets of daily trials. Prism exposure for this latter group was limited to a daily duration of 30 min, corresponding to the time taken to complete the daily tests. Performance improvements as dependent on the interactions in the daily tests could accordingly also be expected for the control group. The temporal aspects and the errors of the performance of the experimental group were contrasted with the performance of the control group by two-way analysis of variance (ANOVA). The subjects completed the four tests without the prisms 3 times: immediately before, immediately after, and 1 week after the study. The performance on day 7 was contrasted with the performance 1 week later (no prisms in either case) by two-way ANOVA in order to investigate postadaptation effects.

To test if visuomotor adaptation (protocols 2–4, below) had an impact on MR performance (protocol 1, below) linear regression analysis was performed on data collected between days 1 and 7. Statistical evaluation of the data was also performed with a *t*-test for paired differences for post hoc comparisons (corrected for multiple comparisons).

Fig. 1 The structure of trials of the MR test (protocol 1)

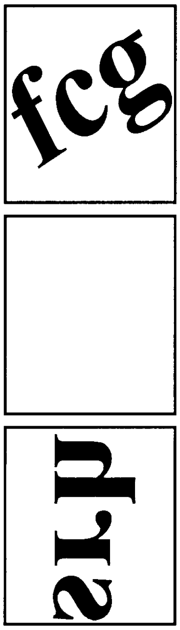


Image is shown for 3000 milliseconds…
Subject decides image is *not reversed* (“normal” to an objective observer) and therefore presses the *left* mouse button.
The response time is measured in milliseconds from the time image is presented.

…a 1000 millisecond pause…
The screen is blank, and the subject waits…

…and then the next image is displayed.
Subject decides image is *reversed* and therefore presses the *right* mouse button.

Protocol 1: mental rotation of alphanumerical characters

The MR of alphanumerical characters as described by Cooper and Shepard (1973) is among the best studied of mental imagery tasks. A salient and consistent finding has been that the RT for a correct judgment is a linear function of the angular difference between a stimulus image, e.g., reversed alphanumerical characters presented with a 45° tilt relative to a normal reference stimulus with 0° rotation (Finke 1989). Such results suggest that an image of the stimulus object is being mentally rotated into congruence with the reference stimulus for the judgment to be made. Earlier work also revealed that subjects spontaneously rotate images to an upright position in this task even without being instructed to do so.

Stimuli and data acquisition

The prism glasses were mounted on a frame so that the subjects could not move their head, only their eyes. The occurrence of systematic eye movements was improbable due to the foveal nature of the fixation task (Richter et al. 2000). The subjects were presented with three-letter combination images on a computer screen. Each image subtended ~5° of visual angle. Half of these were a reversed image of normal characters (reversed), while the rest were normal (i.e., not reversed). These images were also rotated in various angles (in discrete 30° steps starting from 0°). The subject’s task was to determine, as quickly and accurately as possible, if the letters were reversed (from a normal point of view) or not (see Fig. 1). They responded using the computer mouse by pressing one of the buttons. Each day, 200 three-letter words were presented. Each image contained only lower-case nonsense-consonants. Subjects were able to see objects other than the stimulus presented on the screen. In this way an environmental frame of reference could be provided (Soechting and Flanders 1992).

The program used for the data acquisition was written in Microsoft Visual Basic 3.0, and run under Windows 3.1. This program used the Windows API function “GetTickCount,” which was updated once every 55 ms.

Data analysis

The RT was measured for each correct response. Incorrect responses were analyzed separately. Images rotated clockwise and counterclockwise were treated in the same way, as were the reversed and non-reversed images. For each day, a linear regression line (best fit) was calculated between each subject’s RTs and the various stimulus angles. The Y-intercepts, slopes, and Fisher-transformed correlation coefficients, Fisher’s $z=(0.5\ \log([1+r]/[1-r]))$, obtained in this regression analysis were subjected to ANOVA. Because z-transformed correlations are normally distributed, they allow direct comparison of the difference between two correlations (Fisher 1921; Zar 1984). The MR relation was always calculated using the prism (rotated) field of view as the spatial frame of reference.

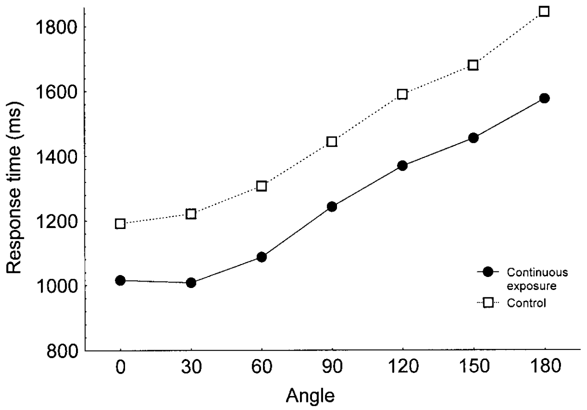


Fig. 2 MR RTs vs rotation angle for days 1–7 (with prisms) combined. The *abscissa* is the angle of the prism-rotated spatial frame of reference

Effects of rotational stimulus angles on MR RTs

All participants could produce the desired MRs without any difficulties. The average of the experimental subjects’ individual mean RT, calculated from the correct responses collected during seven different occasion (days 1–7, prisms), increased systematically, as expected, with increments in stimulus angles (linear regression Y-intercept = 944 ms, slope 3.4 ms/degree, squared product moment correlation coefficient [r^2]=0.95, $P<0.00009$). The same result was also true for the control group (linear regression Y-intercept = 1130 ms, slope 3.7 ms/degree, $r^2=0.97$, $P<0.00003$); see Fig. 2. These results are good evidence that the subjects generally followed the instructions. The mental rotation hypothesis predicts an increase in RT with an increase in the angle of the stimulus because the time taken to rotate a mental image through an angle should be proportional to the angle itself.

Validity of the MR RTs

In order to evaluate the external validity of the RT values employed in the ANOVA, the averaged values (days 1–7 collapsed into one function) were then compared to Cooper and Shepard's (1973) RTs for the identical stimulus angles. The averaged RTs obtained from the present participants (experimental group) plotted against Cooper and Shepard's RTs yielded a product moment correlation coefficient, r_{xy} (x=RTs, protocol 1; y=RTs, Cooper and Shepard 1973), of 0.97 and a linear regression slope of ~1.0. This result gives additional credence to the validity of the present measures and to the procedures employed here to collect the data.

Protocol 2: drawing in templated narrow paths

The subjects were asked to trace patterned narrow paths (mazes) as quickly and accurately as possible. All of the subjects performed the task with their preferred hand. The maze was placed about 40 cm in front of the participants and in the horizontal plane, so that the upper arm was along the trunk and the forearm was approximately horizontal. The patterns were so large that the subjects had to move more than their fingers and wrist to accomplish the task. Typically, the movement involved shoulder and elbow joint rotation, as well as adjustments of the wrist and occasionally of the fingers. The prism glasses were mounted on a frame, so that the subjects could not move their head, only their eyes. The field of view fully encapsulated the drawing area. The subjects were instructed to make an effort to maintain a natural drawing rhythm rather than favoring accuracy at all cost.

The paths were randomly selected from a set of 20 similar paths. All paths had the identical length (40×4 cm) and the same amount of straight parts in each direction. The width of the path was 8 mm. A daily trial ended when the subject had finished two mazes. The average time to complete the two paths and the number of errors were recorded for each participant each day. An error was defined as having occurred when the subject crossed any border.

Protocol 3: dart throwing

Each day, the subjects threw five sets of ten arrows at a dartboard. The dartboard had a diameter of 40 cm, and the subjects stood at a distance of 237 cm from the board (official dart standard). The vertical distance from the floor to the center of the board was 173 cm. The total sum of points scored after each set of ten darts was registered. Generally, the prisms blocked off a sufficiently large part of the peripheral visual field to preclude visual perception of the hand (i.e., the opportunity of in-flight visual feedback was eliminated). The arm movement in this test was therefore controlled by a transformation of the visually coded target into proprioceptive coordinates in limb space (Redding and Wallace 1996).

Protocol 4: whole body ambulation

In the first part of protocol 4, the subjects ambulated forward through a narrow obstacle course turned around and then came back to the start position again (Fig. 3). The path was 50 cm wide and 960 cm long. On both sides of the path, markers were placed that easily fell upon impact. The subjects were instructed to complete the task as quickly and accurately as possible. The second phase of protocol 4 was identical with the first phase, with two important exceptions: (1) the subjects now ambulated sideways, i.e., with one side facing forward in the direction of the walk; and (2) they only ambulated through half of the path. The path was the same as that used in the first phase (Fig. 3). Again, the time to complete the task was recorded, as well as the number of errors.

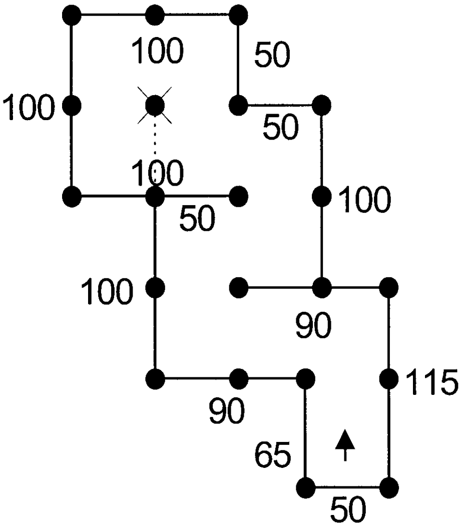


Fig. 3 Obstacle course used in protocol 4. The *numbers* indicate the length of the different sections in centimeters. The *black dots* indicate the position and the approximate size of the markers

Effects of peripheral occlusion on walking time

The confound on walking time represented by the narrowed visual field was assessed in a control test involving three naive subjects and one of the authors, all unpracticed (n=4). When the binocular visual field was restricted to a 55° wide and 32° high aperture, results showed forward ambulation time to be systematically prolonged, from an average of 5.45 s to 6.16 s (P<0.0002, one-tailed paired t-test). The effect of peripheral occlusion alone on walking time appeared therefore relatively negligible (average 11%, STD ±0.09%, range 5–23%).

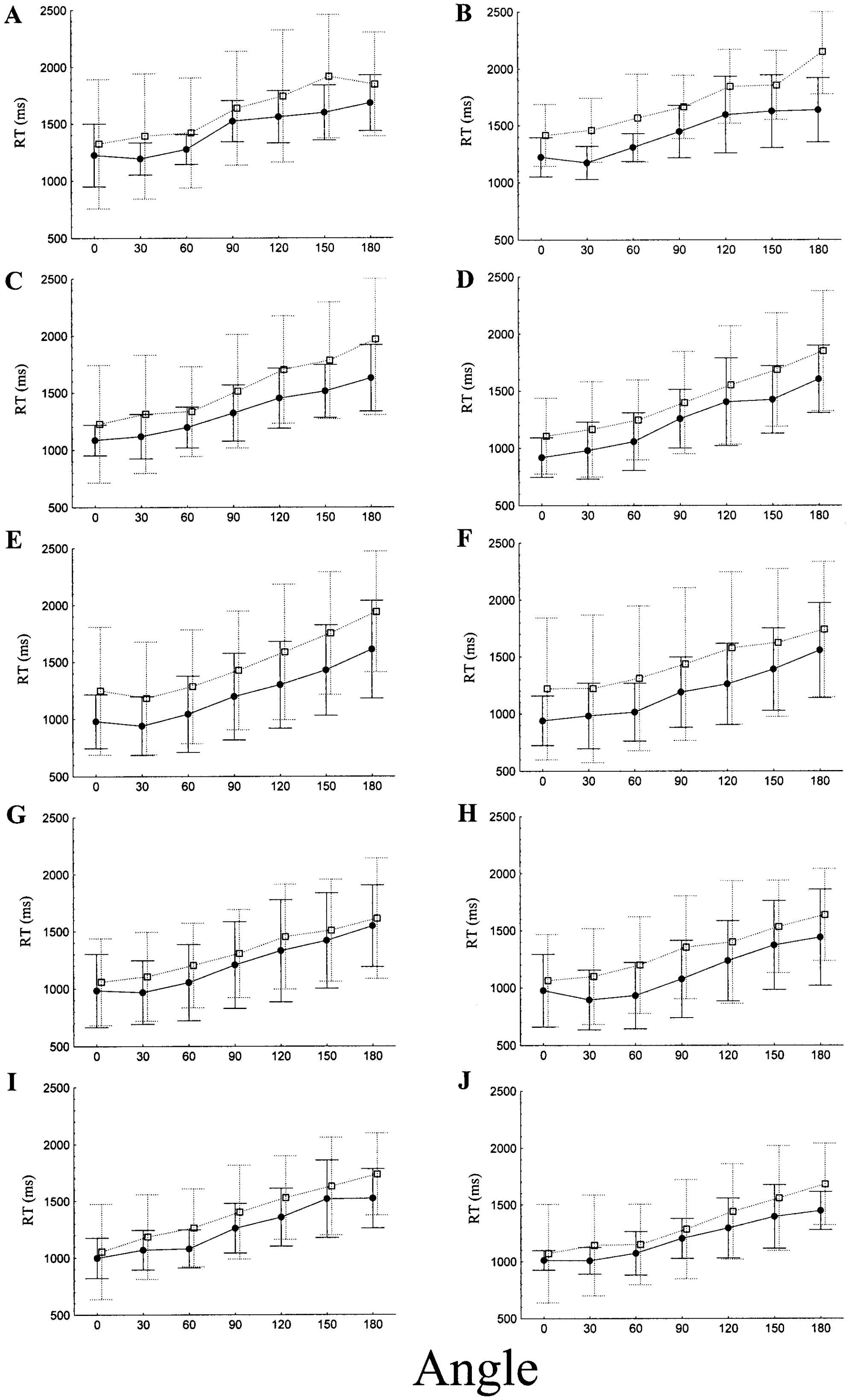
Results

MR functions, days 1–7 (protocol 1)

The unadapted RTs (day 1, prisms) appeared similar to the normal RTs (day 1, no-prisms) with the only exception that subjects now responded within a reversed prism spatial frame of reference rather than congruent with the pull of gravity (Fig. 4A, B). The group-averaged RT of each respective stimulus angle is exhibited in Fig. 4A–J for the successive day (or week) of the experiment. Generally, the MR functions exhibit a positively accelerating increase in RT with angle (although a slight increase in RT sometimes appeared at 0°). The averaged RT (all angles) as well as the rate of errors decreased successively for each day of the experiment (Fig. 5). Error rates ranged between 3% and 26%, showing no significant difference between the two groups and no significant interaction (Fig. 5).

Two-way ANOVA showed a significant main-effect of Day on the MR Y-intercept obtained from the linear regression line calculated between each subject's RT and the various stimulus angles ($F_{(6,72)}$=199789; P<0.0001) (Fig. 6A). No difference between the groups and no interaction was observed. The average Y-intercept for the

Fig. 4A–J Averaged MR RT vs rotation angle for each successive day of prism-induced inversion of the retinal images (*solid circles* continuous exposure, *open squares* control). The *abscissa* is the angle of the prism-rotated spatial frame of reference. *Vertical bars* are standard errors



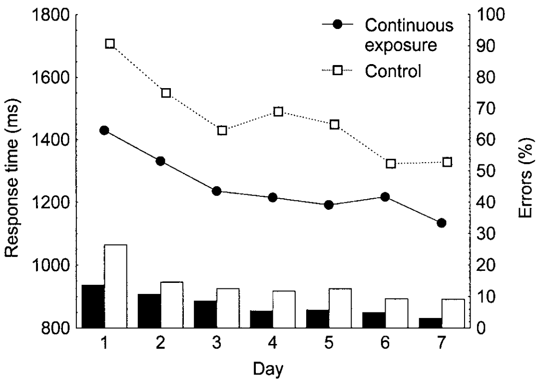


Fig. 5 Averaged MR RT to all rotation angles combined for days 1–7 (with prisms) along with proportion errors (erroneous responses along with no response or "pauses")

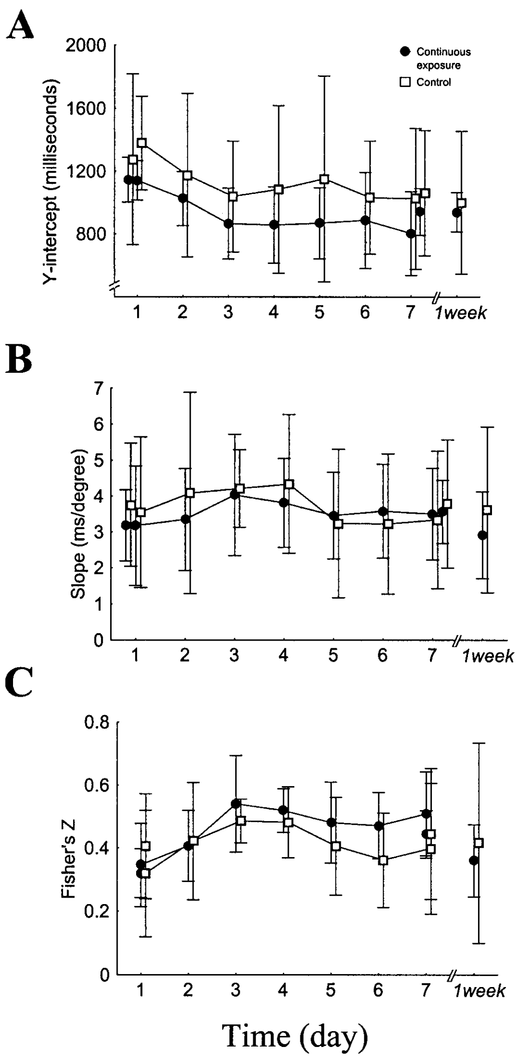


Fig. 6 **A** Time (days) of prism-induced inverted retinal images vs the mean MR Y-intercept. **B** Time (days) vs the mean MR slope. **C** Time (days) vs the mean MR z-transformed correlation coefficient

experimental group (n=7) day 1 was 1140 ms (SE ±47, range 934–1279 ms). By day 7, this value had been reduced to 803 ms (SE ±100, range 498–1275 ms). A drop in mean Y-intercept was observed as early as after 400 trials [two-tailed, paired t-test (n=14), day 1 vs day 2: $P<0.016$]. The Y-intercepts obtained during the 1st day of the experiment were markedly correlated with those obtained during day 7 [r^2: 0.69 (n=14), $P<0.0002$]. This finding, along with a linear regression slope of ~1.0 (x=Y-intercepts day 1; y=Y-intercepts day 7), indicates that the individual values were reliable.

There was no change in slope during days 1–7, nor any significant difference between the experimental and control group, nor any interaction (Fig. 6B). Each day, a 1° turn of the image delayed the RT by ~3.5 ms. An upside-down image thus took more than 0.5 s longer to respond to than an upright image.

There was a significant main effect of Day on the correlation coefficient. The average Fisher-transformed group correlation coefficients increased significantly ($F_{(6,72)}$=4.1; $P<0.05$) (Fig. 6C). Moreover, there was no significant difference between the two groups and no significant interaction.

Drawing, days 1–7 (protocol 2)

The drawing performance improved in a negatively accelerated manner over the course of the 7 days. Two-way ANOVA showed a significant main effect of Group ($F_{(1,12)}$=13,569; $P<0.05$), a significant main effect of Day ($F_{(6,72)}$=36,041; $P<0.0001$), and a significant interaction between Group and Day ($F_{(6,72)}$=1,626; $P<0.005$) (Fig. 7A). Errors rates were reduced for both groups and showed no significant difference between the two groups and no significant interaction (Fig. 7B).

Dart scores, days 1–7 (protocol 3)

The performance in the dart task improved in a positively accelerated manner over the course of the 7 days. Two-way ANOVA showed a significant main effect of Day ($F_{(6,72)}$=2,386; $P<0.0001$) and a significant two-way interaction between Group and Day ($F_{(6,72)}$=673; $P<0.05$) on dart scores. The experimental group's scores generally exhibited the highest values (Fig. 8).

Ambulation, days 1–7 (protocol 4)

Forward ambulation

Administration of the reversing prisms, during day 1, lengthened the forward ambulation time by an average of 92% (±STD 0.04%, range 84–96%). The performance in these trials improved in a negatively accelerated manner over days 1–7. Two-way ANOVA showed a significant main effect of Day ($F_{(6,72)}$=12,459; $P<0.0001$) and a significant interaction between Group and Day ($F_{(6,72)}$=3,318.7; $P<0.01$) with respect to walking time. The experimental group reduced their walking time more than

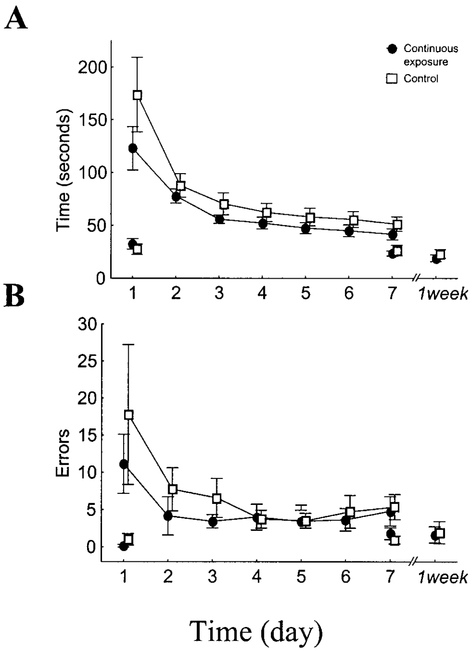


Fig. 7 **A** Time (days) of prism-induced inverted retinal images vs mean time required to complete the tracing of narrow paths. **B** The amount of errors made by the two groups. *Vertical bars* are standard errors

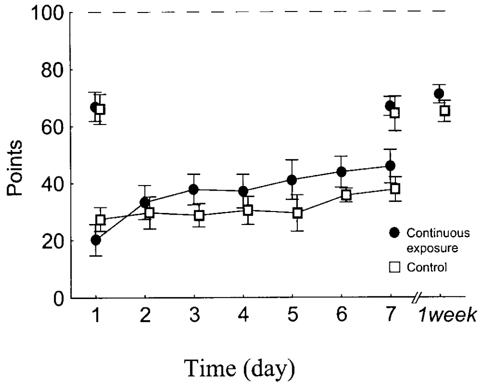


Fig. 8 Time (days) of prism-induced inverted retinal images vs the average number of points scored when throwing darts, and the maximum possible scores (–). *Vertical bars* are standard errors

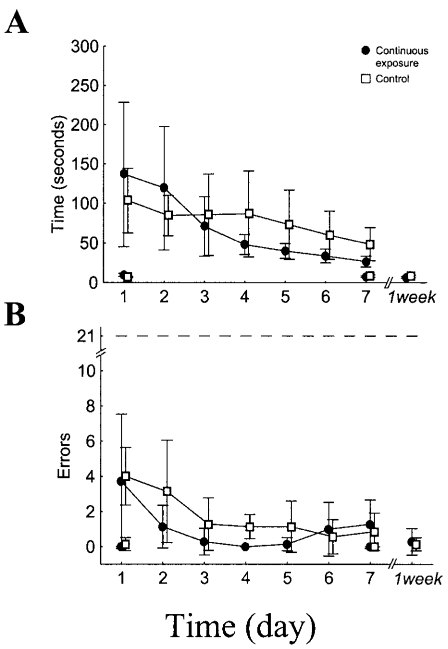


Fig. 9 **A** Time (days) of prism-induced inverted retinal images vs the mean time required to ambulate through a predetermined obstacle course (see Fig. 2). **B** The amount of errors made by the two groups, and the maximum number of possible errors (–). *Vertical bars* are standard deviations

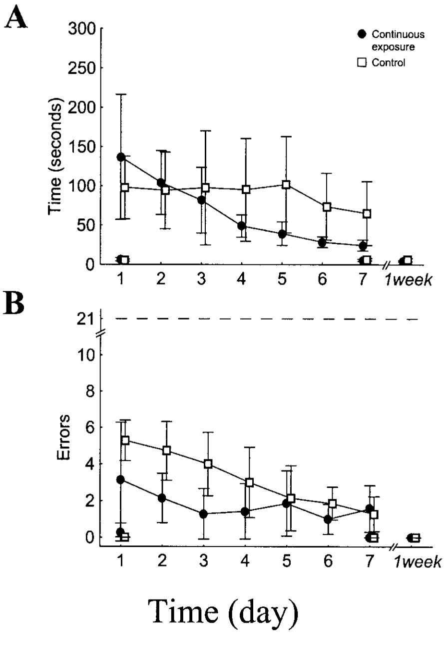


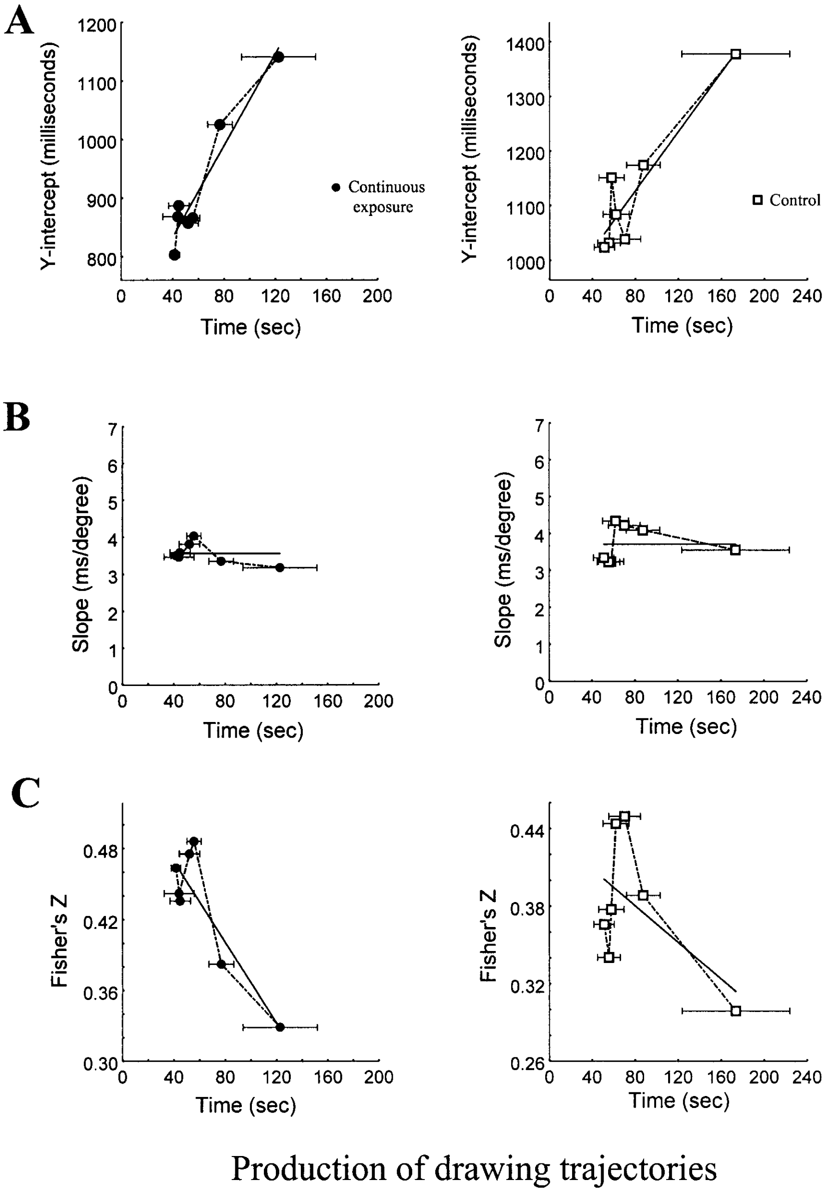
Fig. 10 **A** Time (days) of prism-induced inverted retinal images vs the mean time required to ambulate sideways through half the path. **B** The amount of errors made by the two groups, and the maximum number of possible errors (–). *Vertical bars* are standard deviations

the control group (Fig. 9A). Both groups manifested a reduced number of errors (Fig. 9B). Errors showed no significant difference between the two groups and no significant interaction.

Sideways ambulation

Ambulation time was prolonged by about 50% in comparison to the time measures recorded during forward ambulation. The performance in the sideways ambulation trials improved in a negatively accelerated manner. Two-way ANOVA showed a significant main effect of Day ($F_{(6,72)}$=9,436.8; P<0.0001) and a significant interaction between Group and Day ($F_{(6,72)}$=4,579.8; P<0.0001) on time. The subjects in the experimental group reduced their ambulation time significantly more than the control group (Fig. 10A). Both groups showed a reduced number of errors (Fig. 10B). The experimental subjects made fewer mistakes ($F_{(6,72)}$=2.30; P<0.043) (Fig. 10B).

Fig. 11 Test of the group-averaged relationship between visuomotor adaptation and the MR performance following prism induced inversion of the retinal images (days 1–7). **A** Tracing movements vs *Y*-intercepts. **B** Tracing movements vs slopes. **C** Tracing movements vs Fisher transformed correlation coefficients. *Horizontal bars* are standard deviations. The regression line of the best fit to the data was determined by the method of least squares



Correlations between individual performance in the forward and sideways ambulation trials

The individual time records from the participants (n=14), obtained in the forward ambulation trials, were selectively correlated with the performance acquired in the sideways ambulation trials. The following product moment correlation, r_{xy} (x = forward ambulation time; y = sideways ambulation time), expressed as a coefficient of determination (r^2), was obtained for days 1–7: day 1 without prisms, r^2=0.42 (P<0.01); day 1, r^2=0.11 (P<0.24); day 2, r^2=0.23 (P<0.07); day 3, r^2=0.70 (P<0.0002); day 4, r^2=0.90 (P<0.00001); day 5, r^2=0.79 (P<0.00001); day 6, r^2=0.88 (P<0.00001); day 7, r^2=0.82 (P<0.00001); day 7 without prisms, r^2=0.18 (P<0.13); 1 week later without prisms, r^2=0.68 (P<0.0003).

Postadaptation comparisons

MRs (protocol 1)

No significant main postadaptation effect of Day was apparent on *Y*-intercepts, slopes or Fisher-transformed correlation coefficients. Similarly, no significant effect of Group and no interaction were apparent.

Drawing performance (protocol 2)

There was a significant postadaptation main effect of Day on drawing time ($F_{(1,12)}$=30.90; P<0.001). However, no significant effect of Group and no interaction effect were found. The drawing trials on day 7 immediately after the removal of the glasses were completed at a slower mean rate relative to the trials performed 1 week later (also without prisms) [average (n=14), day 7:50 s; SE ±2.97 s; range 33.6–74.16 s; 1 week later: 42.2 s; SE ±2.91 s; range 23.6–59.31 s].

Dart scores (protocol 3)

No significant main postadaptation effect of Day was apparent on dart scores; and no significant effect of Group and no interaction in the postadaptation comparison were found.

Forward ambulation (protocol 4)

There was a significant main postadaptation effect of Day ($F_{(1,12)}$=12.78; $P<0.005$) on forward ambulation. However, no significant effect of Group and no interaction effect were noted. The forward ambulation trials on day 7 immediately after the removal of the glasses were completed at a slower mean rate relative to the trials performed 1 week later (also without prisms) [average (n=14), day 7: 8.1 s; SE ±0.36 s; range 6.1–10.9 s; 1 week later: 7.4 s; SE ±0.39 s; range 5.5–10.37 s].

Sideways ambulation (protocol 4)

There was a significant main postadaptation effect of Day ($F_{(1,12)}$=6.12; $P<0.05$) on sideways ambulation time. However, no significant effect of Group and no interaction were found. The sideways ambulation trials on day 7 immediately after the removal of the glasses were completed at a slower mean rate relative to the trials performed 1 week later (no prisms) [average (n=14), day 7: 6.22 s; SE ±0.38 s; range 4.2–9.2 s; 1 week later: 5.4 s; SE ±0.48 S; range 3.5–10.72 s).

Relationship between motor adaptation and MR performance, days 1–7

Y-*intercepts*

The experimental groups decrease in Y-intercept correlated with the improvements in: drawing time (r^2: 0.92, $P<0.0006$) (Fig. 11A); dart scores (r^2: 0.85, $P<0.003$); forward ambulation time (r^2: 0.88, $P<0.002$); and sideways ambulation time (r^2: 0.81, $P<0.005$).

Analyses of individual data in the experimental group showed Y-intercepts to decrease in magnitude in a highly individualized, and for four of the seven subjects, noticeably strong temporal correlation with the ongoing rate of visuomotor adaptation in the drawing task (no. 1, r^2=0.96, $P<0.00006$; no. 2, r^2=0.93, $P<0.0005$; no. 3, r^2=0.84, $P<0.004$; no. 4, r^2=0.81, $P<0.006$). Only two out of the seven subjects manifested stable Y-intercepts.

The control group's Y-intercepts correlated only with the reduction in drawing time (r^2: 0.86, $P<0.002$).

Slopes

No correlation could be detected between the slopes and the visuomotor performance improvements (Fig. 11B).

Fisher transformed correlation coefficients

The experimental group's increase in Fisher transformed correlation coefficients correlated with the improvements in: drawing time (r^2: 0.77, $P<0.009$) (Fig. 11C); dart scores (r^2: 0.64, $P<0.03$); forward ambulation time (r^2: 0.67, $P<0.02$); and sideways ambulation time (r^2: 0.56, $P<0.06$).

No correlation could be detected between the control group's Fisher transformed correlation coefficients and the visuomotor performance improvements (Fig. 11C).

Discussion

MR performance during different stages of prism adaptation

The MR RT showed the three following changes. First, it increased in a positively accelerating fashion with an angle relative to a prismatic (reversed) rather than a geocentric spatial frame of reference; second, the Y-intercept of the regression line calculated between each subject's RT and the angles was systematically displaced below the RT of MR made during day 1; and, third, it became progressively more tightly coupled to the stimulus angles. The amount of added processing time that resulted from each added degree of stimulus angle remained constant. These results are discussed separately below.

The 337-ms drop in Y-intercept observed during day 7 (Fig. 4H) relative to the Y-intercept noticed during the 1st day (Fig. 4B) suggests that the relatively more adapted participants were able to perform an extra 96° of MR, because the RT for the 96° rotation angle stimulus during day 7 was equivalent to the RT for the 0° rotation angle stimulus observed during day 1 (linear prediction equation day 1: $0°\times3.17+1{,}140=1{,}140$ ms, day 7; $96.3°\times3.5+803=1{,}140$ ms). The decreased magnitude of the MR Y-intercept is interpreted as resulting from a positive transfer from motor learning. Simple learning effects on the MR performance appear highly unlikely for several different reasons. We would not expect the experimental group's averaged RT decreases to abruptly stop on day 3 and later take off again in almost complete synchrony with the rate of adaptation of the natural motor performance (Fig. 11A). The MR performance of the experimental group was also more tightly coupled to the visuomotor performance than the control group, even though both groups performed an identical number of trials.

Substituting visuomotor adaptation (abscissa in Fig. 11) for the completed number of MR trials (i.e., with a measure of the impact from simple task repetition

Table 1 Comparison of the squared product moment correlation coefficient (coefficient of determination, r^2) computed between the different aspects of the MR performance day 1–7 vs visuomotor adaptation (*left column*), or vs learning from task repetition alone (*right column*)

Y-intercepts vs drawing time			*Y*-intercepts vs number of completed MR trials	
Experimental	0.92	0.0006	0.71	0.016
Control	0.86	0.005	0.57	0.05
Slopes vs drawing time			Slopes vs number of completed MR trials	
Experimental	0.34	0.16	0.43	0.06
Control	0	0.93	0.28	0.22
z-transformed correlation coefficient vs drawing time			*z*-transformed correlation coefficient vs number of completed MR trials	
Group	r^2	*P*	r^2	*P*
Experimental	0.77	0.009	0.41	0.12
Control	0.32	0.18	0	0.91

alone) in the linear regression analysis resulted in a conspicuously weaker relationship to the *Y*-intercepts (and *z*-values) while the slopes remained unaffected (Table 1). The control group's *Y*-intercepts (and *z*-values) remained appreciably less strongly associated with the completed number of MR trials. Analysis of the individual data further verified that *Y*-intercepts (and *z*-values) could decrease in magnitude in a highly individualized and, for some subjects, noticeably strong temporal synchronization with the ongoing rate of visuomotor adaptation. These findings together converge to contradict a main effect from "task repetition alone" and instead point to the conclusion that visuomotor prism adaptation affected the MRs.

That the decreased MR RTs were not due to a trade-off of accuracy for speed is evident from the observation that the RT decreases were accompanied by systematic decreases in errors (Fig. 5) (Wickelgren 1976).

The experimental group's increased correlation between rotational stimulus angle and RT (Fig. 6C) implies that the MR function became progressively more tightly coupled to the stimulus angles. This outcome was in all likelihood caused by the presence of less rotational corrections in the later more primed trials, which would remove variability in the relation between stimulus angle and speed (see Georgopoulos and Massey 1987). Other investigators detailing elementary training effects on the RT, as due to task repetition alone, have not communicated such a systematic increase in the fit of RT data (r^2) to the Cooper and Shepard model (Kail 1986; Leone et al. 1993; Heil et al. 1998).

The MR slopes were unaffected in this experiment. This auxiliary finding implies that the processing constraints responsible for the emergence of the relation between rotational stimuli and RT were unaffected. Thus, the subjects in this study exhibited a constant rate of transforming (rotating) the mental images. This implies that a simple training effect as due to task repetition alone was absent (or alternatively that such effects were cancelled out by administration of the prisms). This result may constitute the most compelling argument against a learning effect from task repetition alone because it is clearly at odds with previous findings where the slope consistently was reported to decrease in magnitude after repetition (Kail 1986; Leone et al. 1993; Heil et al. 1998).

Spatial transformations in the drawing task

The production of drawing trajectories was completed at a successively faster mean rate, through day 1 to day 7, by both the experimental and control group. The results exhibited in Fig. 7 are strikingly similar to those reported by Imamura et al. (1996; cf. their Fig. 1B), who utilized a similar setup, where, on average, seven training trials performed within 1 h were allowed for practice. This gives credence to the validity of the present measures and implies that most of the adaptation took place during task participation, not between the occasions of testing.

The drawing motion of the hand is known to slow down when the path is more curved (Viviani and Terzuolo 1982), and this figural-kinematic relationship is produced centrally by the neural structures generating the instructions that cause the arm to move (Schwartz and Moran 1999). Of note, Pellizzer et al. (1999) showed that while the spatial aspects of the production of drawing trajectories was affected by changes in the correspondence between visual and movement coordinates, the relationship between speed and curvature of the movement trajectory was stable despite drastic changes in this correspondence. Hence, the general saving of time observed in this protocol may be related less to the transformation of the intended direction of movement than to the critical central constraints of the time-consuming and normally effortless processes of planning, initiation, and correction of the intended direction of movement.

Coordination between eye position and synergy of the arm throw

In general, subjects had little difficulty in producing accurate dart scores under normal viewing conditions. However, the prism performance was strikingly poor and remained so throughout the week. The experimental group's (minimal) increases in performance outdid the control group's performance.

Whole body ambulation and adaptation of the vestibulo-ocular reflex

On the 1st day of the study, all subjects exhibited marked difficulties when walking and when orientating their face to targets of interest. Changes in posture and rigidity, as well as slow and poor mobility, were immediate symptoms (cf. Redding and Wallace 1988; Karnath et al. 2000). A closed-loop strategy of walking was adapted: the amplitude of the leg movement was reduced while the frequency thereof was increased, probably so as to maximize visual and tactile feedback. In addition, the visual field was reported as unstable.

The vestibulo-ocular reflex (VOR) plays an essential role in visuospatial perception, as well as in the stabilization of ocular fixation during head movements by ensuring that head movements and eye position in orbit are opposite in direction and of equal amplitude (Robinson 1975; Melvill Jones 1988). The unadapted VOR became very disabling in the walk test, especially when the subject ambulated sideways, due to the occurrence of natural head and neck movements (Crane and Demer 1997). The experience of marked motion discomfort (nausea) was common. On day 3, stabilization of the visual field was reported. Complete reversal of the VOR in the monkey was reported to have been achieved after 2 weeks (Robinson 1975), which is in fair agreement with these results (see also Melvill Jones et al. 1988; Crane and Demer 2000).

Sideways walking time correlated selectively with forward walking time: the preexperimental correlations (day 1, no prisms) broke down after administration of the prisms; successively, after the 3rd day on, these measures became coupled with one another again. Presumably each participant put their similar idiosyncratic signature on time, in both the forward and sideways ambulation trials. When the VOR became unadapted, due to administration of the prisms, this relationship was dissociated. When adaptation of the VOR was obtained, a coupling was observed once again.

Postadaptation comparisons

The relatively modest magnitude decrease in measured performance immediately after the removal of the glasses provides proof for the relative absence of spatial (e.g., cerebellar) alignment (Efstathiou et al. 1967; Glickstein 1992; Seitz et al. 1994; Llinás and Paré 1996; Cordo et al. 1997; Doyon 1997) and instead points to strategic control as the dominating control process (Redding and Wallace 1996). One specific aftereffect, following adaptation of the VOR and removal of the prisms, was an enduring instability of the visual field (Melvill Jones et al. 1988). Moreover, all subjects exhibited agnosia with regards to faces of people known from the experiments.

Relationship between visuomotor adaptation and MR performance

A conspicuous and previously unprecedented finding in this study was that visuomotor prism adaptation was highly correlated with simultaneously occurring decreases in MR *Y*-intercepts and with increases in MR correlation coefficients (while MR slopes remained stable). The successive performance improvements evident in the production of drawing trajectories on days 1–7 were most strongly associated with these aspects of the MR performance (Fig. 11). These results corroborate recent studies that demonstrated that certain aspects of the MR performance share common aspects with the process of real (natural) movements (Georgopoulos et al. 1986; Schwartz et al. 1988; Finke 1989; Pellizzer and Georgopoulos 1993; Bonda et al. 1995; Georgopoulos and Pellizzer 1995; Georgopoulos et al. 1995; Parsons et al. 1995; Pellizzer et al. 1995; Wexler et al. 1998; Ganis et al. 2000) as well as studies demonstrating that effects by a prism adaptation includes aspects of mental imagery (Farne et al. 2001; Tilikete et al. 2001; Rode et al. 2001).

It is suggested that these results reflect an improved attentional (strategic) ability to replace incorrect (error producing) control signals with correct (error reducing) control signals. As a result, perceptual-motor start-up processes directly related to spatial coding and to the planning, initiation and correction of the intended direction of motor or mental movement improved, while the subprocess ("stage") (Sternberg 1969) concerned with transformations of such movements remained unchanged. Several hypotheses can be made to explain the results. One is that a common brain structure is accessed jointly by the visual and motor systems in the preparation for mental rotation and that experience-dependent plasticity in this structure formed the basis of the common performance improvements. A candidate locus for such processes may reside in the posterior parietal cortex (Batista and Andersen 2001). In the network of cortical areas activated by MR, the posterior parietal cortex upholds a prominent standing (Alivisatos and Petrides 1996; Cohen et al. 1996; Tagaris et al. 1996; Richter et al. 2000). This structure has repeatedly been implicated in recalibration of visually guided reaching following administration of displacing prisms (Clower et al. 1996). Adaptation to a visual distortion is also known to provide an efficient and fast way (minutes) to stimulate neural circuitry responsible for the transformation of sensorimotor coordinates in this very same cortical area.

Specifically, Rossetti et al. (1998) communicated in an earlier study, concerned with right hemisphere stroke patients and effects of prism adaptation to a rightward optical deviation, that <5 min of prism exposure was enough to obtain aftereffects on the organization of higher levels of spatial representations. Additional recent studies, from the same group of scientists, clearly demonstrate that effects by a single short duration, <20 min of prism adaptation, are spread over a wide range of visuomotor functions including mental imagery (Farne et al. 2001; Rode et al. 2001; Tilikete et al. 2001).

General conclusions

The types of visuomotor failures during the early stages of the experiment resembled those reported to be seen in ideomotor/ideational apraxia (Yudofsky and Hales 1992; McDonald et al. 1994; Leiguarda and Marsden 2000) and/or those associated with cerebellar lesions (Thatch 1997). Two error patterns could be distinguished: (1) inaccurate attempts to execute the movements. Movements were spatially disoriented, incomplete in production, or clumsy. (2) Episodic evocation errors, whereby the subjects seemingly could not conjure up a conception of the movement and therefore "did nothing" (paused). By the third day, almost all of the visuomotor adaptation-functions leveled off (cf. Karni and Sagi 1993).

The occurrence of small magnitude postadaptation aftereffects points to some degree of adaptive spatial (e.g., cerebellar) alignment but more strikingly links the adaptation with strategic control and with substantially improved perceptual-motor start-up processes (Redding and Wallace 1996).

The result that increases in natural motor proficiency were accompanied by a systematic and noticeable decrease in magnitude of the MR *Y*-intercept and by increases in the MR correlation coefficient indicates that visuomotor adaptation to inverting prisms engages, and thereby stimulates, a cortical system also invoked in the preparatory process of MR. As a result perceptual-motor start-up processes directly related to spatial coding and to the planning, initiation and correction of the intended direction of motor-or-mental movement improved while the subprocess ("stage") concerned with transformations of such movements remained unchanged.

Despite an opportunity for prolonged prism adaptation, subjects never reported the environment to appear upright and consistent with the sensory input transmitted through other modalities. These anecdotal reports are fully consistent with results reported by Linden et al. (1999). The perceptual effects caused by inverting prisms seem out of range for physiological correction (see Singer et al. 1979; Sugita 1996).

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