

Enhancing Visuomotor Adaptation by Reducing Error Signals: Single-step (Aware) versus Multiple-step (Unaware) Exposure to Wedge Prisms

Carine Michel^{1,3}, Laure Pisella¹, Claude Prablanc¹, Gilles Rode^{1,2},
and Yves Rossetti^{1,2}

Abstract

■ Neglect patients exhibit both a lack of awareness for the spatial distortions imposed during visuomanual prism adaptation procedures, and exaggerated postadaptation negative after-effects. To better understand this unexpected adaptive capacity in brain-lesioned patients, we investigated the contribution of awareness for the optical shift to the development of prism adaptation. The lack of awareness found in neglect was simulated in a multiple-step group where healthy subjects remained unaware of the optical deviation because of its progressive stepwise increase from 2° to 10°. We contrasted this method with the classical single-step group in which subjects were aware of the visual shift because they were directly exposed to the full 10° shift. Because the number of pointing trials was identical in the two groups, the total amount of

deviation exposure was 50% larger in the single-step group. Negative after-effects were examined with an open-loop pointing task performed with the adapted hand, and generalization was tested with open-loop pointing with the nonexposed hand to visual and auditory targets. The robustness of adaptation was assessed by an open-loop pointing task after a simple de-adaptation procedure. The progressive, unaware condition was associated with larger negative after-effects, transfer to the nonexposed hand for the visual and auditory pointing tasks, and greater robustness. The amount of adaptation obtained remained, nevertheless, lower than the exaggerated adaptive capacity seen in patients with neglect. Implications for the functional mechanisms and the anatomical substrates of prism adaptation are discussed. ■

INTRODUCTION

Under normal conditions, our different sensory modalities provide spatial inputs which are kept aligned. This alignment can be perturbed, however, when the spatial location of visual stimuli is altered by means of mirrors (e.g., Sanes, Dimitrov, & Hallett, 1990), video devices (e.g., Ingram et al., 2000), or optical prisms (e.g., Rossetti, Desmurget, & Prablanc, 1995; Redding & Wallace, 1988). Prism adaptation has been used to study short-term visuomotor plasticity since the 19th century (Stratton, 1896). Because it is not clear whether complex visual field modifications such as left–right inversion or up–down reversal give rise to simple visuomotor adaptation or to other more complex processes, most studies have explored adaptation to wedge prisms that produce a homogenous optical shift of the visual field. The classical procedure for adaptation consists of pointing to visual

targets while wearing prisms that deviate the visual field laterally. At the beginning of the exposure, subjects produce dynamic and endpoint errors in the direction of the optical shift. On the basis of feedback about these error signals, subjects gradually improve their performance until they achieve accurate behavior. This phase of the prism exposure is called the *error reduction phase*, in which visuomotor practice leads to new sensorimotor correlations being established. When the prisms are removed after adaptation, the sensorimotor correlations again become inappropriate and the subject's pointing movements are shifted in the direction *opposite* to the prismatic shift. This postadaptation shift is named the *compensatory or negative after-effect*. The entire process is a form of sensorimotor adaptation. Two main parameters are used to characterize the subjects' reactions to prism exposure, corresponding to the two main periods of the adaptation process: first, the progressive pointing error reduction during prism exposure and second, the negative after-effects measured by the difference between visual pointing performance tested post- and pre-adaptation. The error reduction was initially attributed to a *strategic component* of the adaptation processes (Welch, Choe, & Heinrich, 1974). Weiner, Hallett, and

¹INSERM U864, Espace et Action, Bron, France; Université Claude Bernard, Lyon 1; Institut Fédératif des Neurosciences de Lyon (IFNL), Lyon, France, ²Hospices Civils de Lyon, Mouvement et Handicap, Hôpital Henry Gabrielle and Hôpital Neurologique, Lyon, France, ³INSERM ERM 207, Motricité-Plasticité, Université de Bourgogne, Dijon, France

Funkenstein (1983) considered this phenomenon as a form of cognitive correction, and Redding and Wallace (1996, 2002) viewed it as “strategic perceptual–motor control.” More recently, Redding, Rossetti, and Wallace (2005) have proposed that this aspect of prism adaptation be depicted as “recalibration.” Not only during but also beyond this initial period of prism exposure, further pointing movements involving an *adaptive component* are necessary to fully develop true adaptation (Rossetti, Koga, & Mano, 1993; Weiner et al., 1983) or “adaptive realignment” (Redding et al., 2005). This adaptive component not only participates in part of the error reduction but is also largely responsible for the negative after-effects. Strategic recalibration and adaptive realignment components both contribute to the adapted behavior at the end of the exposure (Redding et al., 2005).

To demonstrate unambiguously the existence of two such separate contributions to prism adaptation, it is necessary to isolate these two components. If one of the two components can be inactivated, then the other one should be responsible for the entire compensation. An analysis of the literature shows that the respective contribution of the two components to the entire compensation can vary. For example, when there is a strong strategic component such as what occurs with reversed vision (e.g. Richter et al., 2002; Stratton, 1896), no after-effect is observed. Similarly, when the contribution of the strategic component is increased by making subjects aware of the distortion during lateral shifts of the visual field (by providing them with explicit information about the prisms), after-effects are reduced (Jakobson & Goodale, 1989). Conversely, when the strategic component is impaired, for example, due to reduced cognitive ability in the elderly, error reduction becomes slower and after-effects are not only greater (Weiner et al., 1983) but also longer-lasting (Fernandez-Ruiz, Hall, Vergara, & Diaz, 2000). In line with these results, Kagerer, Contreras-Vidal, and Stelmach (1997) have shown that gradually increasing visuomotor distortion by rotated visual feedback leads to greater adaptation than a sudden exposition to the full distortion. The performance of neglect patients is also relevant. Typically, in unilateral spatial neglect, the left side of space is neglected after right brain damage (Halligan, Fink, Marshall, & Vallar, 2003). Although prism after-effects in healthy subjects do not last longer than several minutes (e.g., Welch et al., 1974), and are typically not greater than 50% of the prismatic deviation (e.g., Efstathiou, 1969), after-effects in neglect patients have been reported to last 2 hours (Rossetti et al., 1998), 1 day (Farnè, Rossetti, Toniolo, & Làdavas, 2002), or even 4 days (McIntosh, Rossetti, & Milner, 2002; Pisella, Rode, Farnè, Boisson, & Rossetti, 2002). Interestingly, the magnitude of the adaptation in neglect patients also seems to reach 75% of the optical deviation (Rossetti et al., 1998). These markedly increased after-effects may be linked with a surprising “hyperosognosia” (self-attribution of the prism-induced errors) for the sensorimotor perturba-

tion introduced by the prisms (Rode, Pisella, Rossetti, Farnè, & Boisson, 2003). Patients do not overtly (neither spontaneously nor following direct questioning) detect the visual perturbation, which is known to induce a spontaneous surprise reaction in healthy subjects. Further, patients do not show any skin conductance modifications when prisms are unexpectedly introduced in the course of a pointing task (Calabria et al., 2004).

In the present experiment, we attempted to simulate in healthy subjects the lack of awareness seen in neglect patients in order to isolate the contribution of the adaptive realignment component during prism adaptation. Subjects were exposed to the optical deviation usually used for neglect rehabilitation (10° rightward deviation) to investigate whether the lack of awareness can fully explain the exaggerated adaptive capacity of neglect patients. In a “multiple-step” condition, neglect-like unawareness of the optical shift was achieved by progressively increasing the lateral visual shift from 2° to 10° in steps of 2°. This multiple-step condition was compared with a classical “single-step” condition in which the lateral visual shift was always 10° during the exposure period. The two experimental conditions were designed to assess the contribution of the strategic recalibration component by keeping the number of trials constant. Consequently, and importantly, the absolute amount of exposure to the visual shift was greater in the single-step group than in the multiple-step group. The quantity of exposure was measured by the number of trials subjects were exposed to, multiplied by the number of degrees of optical shift (i.e., 84 trials × 10 degrees = 840 trial-degrees for the single-step group vs. only 560 trial-degrees for the multiple-step group, i.e., 50% more trial-degrees in the single-step group). The present study therefore investigated whether quantitatively reduced exposure (multiple-step group) would lead to less adaptation or whether the lack of awareness of the sensorimotor conflict obtained in this condition would lead to more adaptation. On the basis of the neglect patients’ super-adaptation, the multiple-step group may even lead to a larger amount of adaptation despite its reduced level of exposure.

METHODS

Subjects

Twenty-eight right-handed and normally sighted healthy subjects participated in the experiment. The multiple-step group was performed by a group of subjects composed of nine women and five men, ranging in age from 20 to 32 years (mean = 25 years, *SE* = 1.0 years). The single-step group was performed by a group of subjects also composed of nine women and five men, ranging in age from 19 to 34 years (mean = 24 years, *SE* = 1.3 years). All subjects gave their informed consent prior to their inclusion in the study, in accordance with the local ethics committee.

Apparatus

The apparatus used in this experiment was similar to that employed by Rossetti et al. (1998). The subject was comfortably seated in a chair. The position of the chair was fixed so that the participant could comfortably rest his head in a chin-rest. The measurement apparatus consisted of a two-layer rectangular black wooden box-like frame (30 cm high, 80 cm wide, and 80 cm deep) placed on a table and open on the side facing the subject. A loudspeaker used to produce white noise and a red LED were placed in front of the subject at eye level (80 cm in front of the eyes). Throughout the experiment, the subject was seated in front of the apparatus, and placed his arms within the frame. The head was kept aligned with the body axis using the chin-rest situated on the upper edge of the box. At the start of each trial, the subject's hand was placed on a piece of foam on the lower layer of the frame near the sternum. During the prism adaptation procedure, the starting hand position and first 15 cm of the pointing surface were occluded from the subject's view. The hand was visible during the remaining part of the trajectory throughout adaptation (concurrent exposure procedure) because the top of the box was open on the distal end. The subject was required to point to one of two visual targets (in a random order) on the lower surface of the box, and then return to the starting position after each trial. Before each trial, the target was verbally indicated by the experimenter. The two visual targets were colored sticker dots (diameter 6 mm) placed at 10° to the right and to the left of the body midline within reaching distance (30 cm away from the starting hand position). The lower surface of the box was lined with black carbon-impregnated paper (80 cm \times 80 cm), which permitted an electrical current to be passed across it. To measure the endpoint of the pointing movements, the subject wore a metal thimble on the index finger of his right hand. The thimble and the active surface of the box were connected to a liquid crystal display, which provided a digital readout of the endpoint. This apparatus produced measurements with an accuracy of 0.1° .

Experimental Procedure

The experimental procedure can be divided in three classical periods: pretest, prism exposure, and posttest. Pre- and posttests were composed of the same tasks performed in the following order: auditory open-loop pointing and visual open-loop pointing. All pre- and posttests were performed in darkness.

For the visual and the auditory open-loop pointing tasks, the subject was required to point in vertical alignment with the single central LED or the loud speaker on the lower surface of the box. The visual and auditory targets were presented at the objective straight-ahead

of the subject and out of the reaching distance of the pointing limb (80 cm). The adaptation procedure was performed with the right hand. Left (unexposed) and right (exposed) hands were used successively with 12 trials each in visual and auditory pointing tasks in order to assess the level of intermanual transfer of adaptation. As mentioned above, the tasks comprising the pretest were composed of the auditory open-loop pointing task and the visual open-loop pointing task (VP1). The auditory pretest was performed before the visual pretest. Visual open-loop pointing tasks were performed at the end of the adaptation procedure (VP2), following auditory open-loop pointing tasks (VP3) and also after a 2-min rest in darkness (VP4). The robustness of the adaptation was assessed by an additional procedure. The subject was exposed to a short de-adaptation session during which 10 pointing trials were performed in a closed-loop condition without prisms (i.e., exposure to normal vision). Then a final visual open-loop pointing task was performed (VP5).

The "single-step" adaptation group used a single-step exposure to the 10° rightward shift. The iterative increment of the 2° rightward lateral visual shift of the "multiple-step" adaptation group was achieved with prisms producing progressive visual shifts of 2° , 4° , 6° , 8° , and 10° in one group of subjects. The wedge prisms were fitted into Cebe glacier goggles to induce a right displacement of the visual field (Optique Peter, Lyon, France; <http://optiquepeter.com>). Each circular eyepiece contained a clear wedge prism that displaced the visual field horizontally. Black leather covers attached to the temporal and nasal portions of the frames ensured that subjects could not see any undistorted portions of the peripheral visual field. The weight of the five prisms with different visual shifts was made identical by loading the prisms with small pieces of lead in order to reduce cognitive cues about changes in the prisms between exposure sessions. The experimental procedure of the multiple-step group was as follows. There were 84 pointing trials during prism exposure. Short breaks were made after trial numbers 14, 28, 42, 56, and 84 in order to change the goggles. The subjects wore 2° deviating prisms (until trial 14), 4° deviating prisms (until trial 28), 6° deviating prisms (until trial 42), 8° deviating prisms (until trial 56), and 10° deviating prisms (until trial 84). The experimental procedure of the single-step group was similar: During short breaks, the same 10° deviating prisms were removed to mimic the change of prisms of the multiple-step group. The two experimental conditions had the same number of trials (84 trials), but the total quantity of visual shift exposure differed. The quantity of visual shift exposure was measured by multiplying the quantity of visual shift (in degrees) by the number of pointing trials. This quantity was 840 trial-degrees in the single-step group ($10^\circ \times 84$ trials) and 560 trial-degrees in the multiple-step group ($2^\circ \times 14$ trials + $4^\circ \times 14$ trials + $6^\circ \times 14$ trials + $8^\circ \times 14$ trials + $10^\circ \times 28$ trials).

Analysis

For visual and auditory open-loop pointing tasks, the pointing errors were measured as the angle between the recorded pointing position and the target position (or the absolute straight-ahead), with respect to the start position. Leftward errors were assigned a negative value and rightward errors a positive value. Performance lying out of the range of the mean ± 1.96 standard deviation was excluded from statistical analysis (a total of 2.2% of the trials). This procedure was not applied to the analysis of the pointing trials during session VP5 because a significant trial rank effect was observed.

In order to test for the presence of after-effects in the two groups of subjects, means were calculated for each task and compared as a within-subject factor between the two sessions (pre- and posttest), whereas the adaptation group (multiple-step and single-step) were compared as a between-subjects factor in a two-way repeated measures analysis of variance (ANOVA). To analyze the transfer of adaptation in the two groups, the hand used to evaluate after-effects was included as a factor in all of the relevant ANOVAs. The decay of adaptation between the two groups throughout the sessions (VP2 to VP5) was also analyzed by a repeated measures ANOVA. Specific differences between the levels of each factor were analyzed using least-significant-difference post hoc comparisons. To test whether there was a p in the two groups, we also performed a multivariate analysis of variance (MANOVA), including “modality,” “hand,” and “adaptation” as variables.

In order to ensure that the initial pretest performance was not different between the two adaptation groups, a t test was performed.

All statistics were performed with the STATISTICA software package (release 5.5, 1999). Group means (\pm standard errors) are presented in the Results section.

RESULTS

Before the quantitative description of the results, several qualitative observations can be made. During prism exposure, all subjects wore prisms of the same weight, but differing in the degree of optical deviation. In the single-step group, subjects spontaneously expressed their surprise during the first pointing trial(s). On the contrary, in the multiple-step group, subjects did not report that the prisms were responsible for any visual shift, even when specifically questioned at the end of the experiment. When subjects were persistently questioned about differences between the different prisms in the multiple-step group, several subjects mentioned a difference in weight between several prisms (which was actually not the case), suggesting that their attention had not been directed to the optical shift.

The pretest performance for all tasks was not different between the two groups of adaptation (all $t > -1.5$, $p > .12$).

After-effect in the Visuomotor Coordination

Visual Open-loop Pointing with the Right Hand (VP1, VP2)

Performance of subjects varied according to the group of adaptation (Figure 1, Figure 5, Table 1). In the multiple-step group, the mean value in the pretest (VP1) was $0.7^\circ \pm 0.82^\circ$. The mean value in the posttest (VP2) was $-4.9^\circ \pm 0.84^\circ$. In the single-step group, the mean value in the pretest (VP1) was $0.6^\circ \pm 0.63^\circ$ and was $-3.4^\circ \pm 0.48^\circ$ in the posttest (VP2). The repeated measures ANOVA on the mean values showed a significant effect of adaptation [$F(1,26) = 168.48$, $p < .001$], and a significant interaction between adaptation and group [$F(1,26) = 4.84$, $p < .04$]. These results revealed a greater amplitude of negative after-effect for open-loop pointing in the multiple-step group than in the single-step group. The difference between posttest and pretest was $-5.6^\circ \pm 0.60^\circ$ in multiple-step group, whereas it was only $-4.0^\circ \pm 0.44^\circ$ in the single-step group. Post hoc comparisons showed a significant effect of adaptation in both groups ($p < .001$).

Visual Open-loop Pointing Task with the Left Hand

Transfer of adaptation to the left nonexposed hand differed according to the group (Figure 2, Figure 5, Table 1). The mean value of the multiple-step group was $1.5^\circ \pm 0.83^\circ$ in the pretest and $0.1^\circ \pm 1.17^\circ$ in the

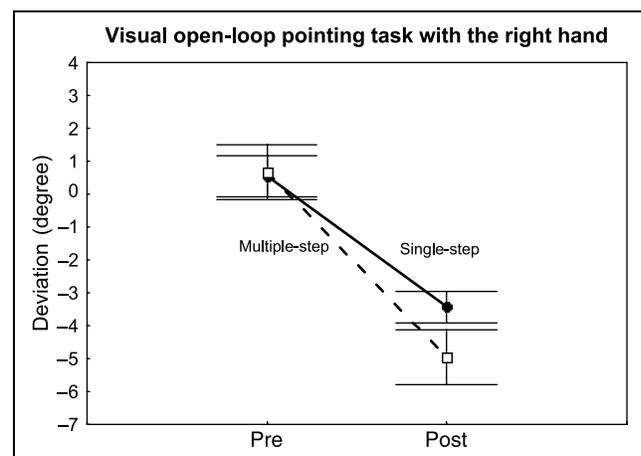


Figure 1. Visual open-loop pointing task with the right hand in VP1 (pretest) and in VP2 (posttest) for both groups. Plain line shows the performance of the single-step group and the dotted line shows the performance of the multiple-step group. The amplitude of adaptation is larger in the multiple-step group than in the single-step group.

Table 1. Main Results of ANOVA Analysis for Visual and Auditory Pointing Tasks with the Right and Left Hands

<i>Variables</i>	<i>Main Results: ANOVA and Post Hoc Comparisons</i>
Visual open-loop pointing task with the right hand	<ul style="list-style-type: none"> – effect of adaptation (ANOVA) – interaction Adaptation * Group (ANOVA) – effect of adaptation in both groups (post hoc) – difference between the two groups (ANOVA on after-effects)
Transfer to visual open-loop pointing task with the left hand	<ul style="list-style-type: none"> – effect of hand (ANOVA) – effect of adaptation (ANOVA) – interaction Adaptation * Group (ANOVA) – interaction Hand * Adaptation (ANOVA) – effect of adaptation for the left hand only in the multiple-step group (post hoc)
Auditory open-loop pointing task with the right hand	<ul style="list-style-type: none"> – effect of adaptation (ANOVA) – effect of adaptation in both groups (post hoc)
Transfer to auditory open-loop pointing task with the left hand	<ul style="list-style-type: none"> – effect of hand (ANOVA) – effect of adaptation (ANOVA) – effect of adaptation for the left hand only in the multiple-step group (post hoc)
Decay of adaptation throughout VP2, VP3, VP4, and VP5 sessions	<ul style="list-style-type: none"> – effect of session (ANOVA) – interaction Group * Session (ANOVA) – decrease of adaptation between VP2 and all the other sessions in both groups (post hoc) – decrease between VP3 and VP5 in the single-step group (post hoc)
Robustness of adaptation during VP5 session	<ul style="list-style-type: none"> – greater strengthening of adaptation throughout VP5 trials in the multiple-step group (variable of de-adaptation compared to zero).

Main effects and interactions are presented. Specific effects of adaptation in both groups were provided by post hoc comparisons (all effects at $p < .05$).

posttest. The difference between the posttest and pretest was $-1.4^\circ \pm 0.69^\circ$ (i.e., 25% of the total shift found for the adapted hand in this group). In the single-step group, performance was $1.5^\circ \pm 0.97^\circ$ in the pretest and $1.0^\circ \pm 0.58^\circ$ in the posttest. The difference between posttest and pretest was $-0.5^\circ \pm 0.68^\circ$ (i.e., 12.5% of the total shift in this group). ANOVA testing intermanual transfer with “hand” as a factor showed a significant effect of hand [$F(1,26) = 16.94, p < .001$], a significant effect of adaptation [$F(1,26) = 105.17, p < .001$], and significant interactions between adaptation and group [$F(1,26) = 4.8, p < .04$], and between hand and adaptation [$F(1,26) = 37.04, p < .001$]. Post hoc comparisons showed a significant effect of adaptation for the left hand only in the multiple-step group ($p < .001$). These results suggested that a significant transfer to

the nonexposed hand occurred only in the multiple-step group.

Generalization to the Auditory Modality

Auditory Open-loop Pointing Task

Performance with the right hand was similar in the single-step and multiple-step groups (Figures 3–5, Table 1). The mean value was $-0.7^\circ \pm 1.52^\circ$ in the pretest and $-3.3^\circ \pm 1.37^\circ$ in the posttest of the multiple-step group (difference = $-2.6^\circ \pm 1.24^\circ$). The mean value of the single-step group was $-1.5^\circ \pm 1.67^\circ$ in the pretest and $-4.9^\circ \pm 1.63^\circ$ in the posttest (difference = $-3.4^\circ \pm 0.95^\circ$) (Figure 3). The repeated measures ANOVA showed a significant effect of adaptation [$F(1,26) = 14.85; p <$

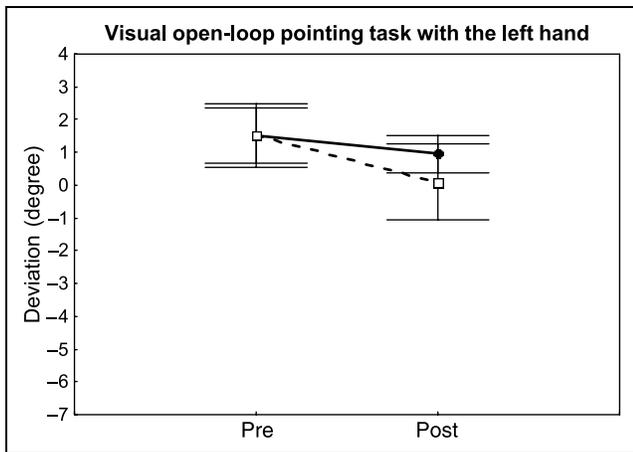


Figure 2. Visual open-loop pointing task for the left hand in pretest and posttest for the single-step group (plain line) and for the multiple-step group (dotted line). The transfer to the nonexposed left hand occurs only in the multiple-step group.

.001]. Post hoc comparisons showed a significant effect of adaptation in both groups (both $p < .03$).

Performance with the left hand differed according to the group. The mean value was $2.2^\circ \pm 1.13^\circ$ in the pretest and $-1.4^\circ \pm 2.08^\circ$ in the posttest of the multiple-step group (difference = $-3.6^\circ \pm 2.00^\circ$). The mean value of the single-step group was $0.5^\circ \pm 2.03^\circ$ in the pretest and $0.3^\circ \pm 2.21^\circ$ in the posttest (difference = $-0.2^\circ \pm 0.67^\circ$) (Figure 4). When transfer to the left unexposed hand was analyzed using “hand” as a factor, there was a significant effect of hand [$F(1,26) = 9.67$, $p < .005$] and a significant effect of adaptation [$F(1,26) = 13.60$, $p < .005$]. No interaction between hand and adaptation was observed [$F(1,26) = 0.78$, $p > .3$]. Post

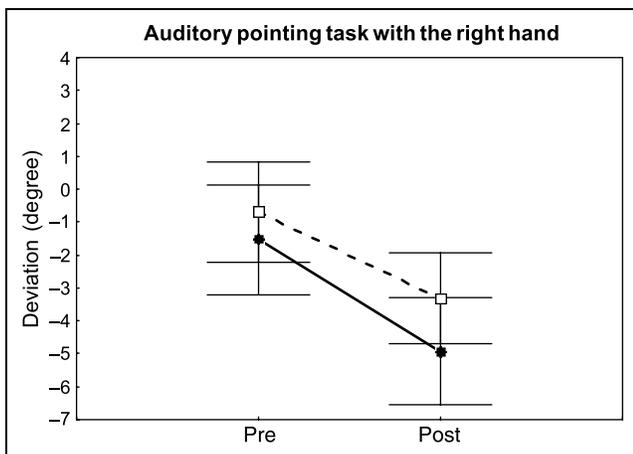


Figure 3. Auditory open-loop pointing task with the right hand in pretest and posttest for the single-step group (plain line) and for the multiple-step group (dotted line). Performance is similar in the single-step and multiple-step groups.

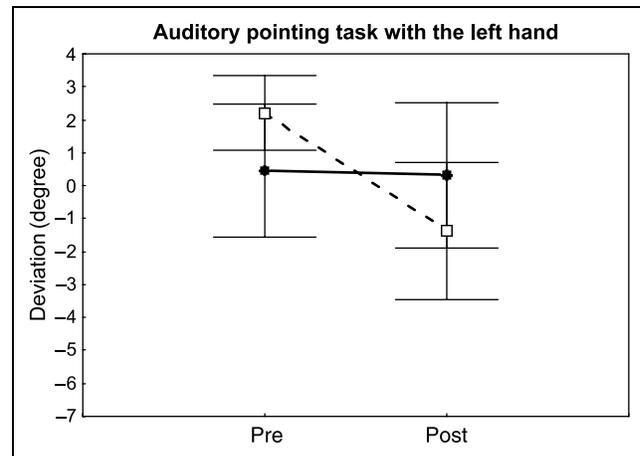


Figure 4. Auditory open-loop pointing task with the left hand in pretest and posttest for the single-step group (plain line) and for the multiple-step group (dotted line). Only the multiple-step group exhibits a significant effect of adaptation.

hoc comparisons showed a significant effect of adaptation for the left hand only in the multiple-step group ($p < .02$). A MANOVA including “modality,” “hand,” and “adaptation” as factors showed a significant effect of hand [$F(1,26) = 15.68$, $p < .001$], a significant effect of adaptation [$F(1,26) = 45.76$, $p < .001$], and a significant interaction between hand and adaptation [$F(1,26) = 10.07$, $p < .005$].

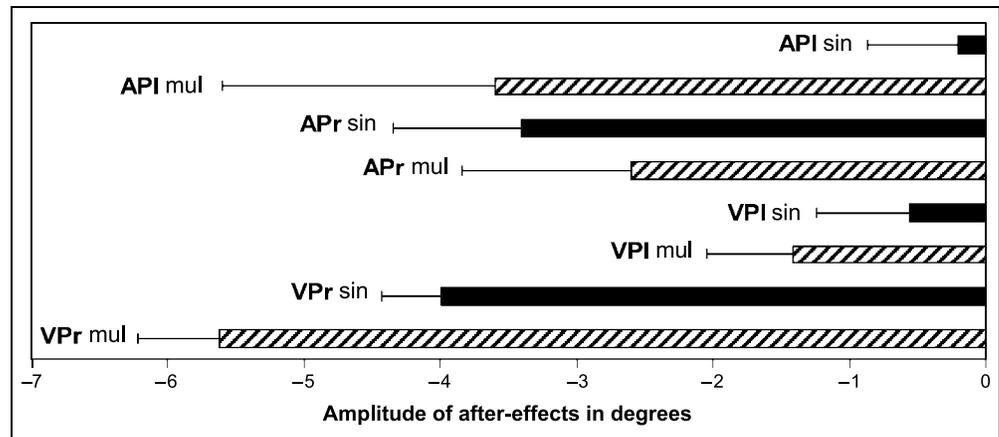
To sum up, for auditory open-loop pointing task, the multiple-step group showed a significant effect of adaptation with both hands, whereas the single-step group exhibited an effect of adaptation only with the adapted right hand.

Decay of Adaptation from VP2 to VP5 and Robustness of Adaptation during VP5

Decay of Adaptation

The decay of adaptation concerned the decrease in amplitude of after-effects following the adaptation procedure. In the multiple-step group, the amplitude of after-effects was $-4.9^\circ \pm 0.84^\circ$ in VP2, $-1.7^\circ \pm 0.98^\circ$ in VP3, $-2.3^\circ \pm 1.14^\circ$ in VP4, and $-2.2^\circ \pm 0.18^\circ$ in VP5. In the single-step group, after-effect amplitude was $-3.4^\circ \pm 0.48^\circ$ in VP2, $-2.3^\circ \pm 0.57^\circ$ in VP3, $-2.1^\circ \pm 0.48^\circ$ in VP4, and $-1.2^\circ \pm 0.22^\circ$ in VP5. ANOVA testing the decrease in amplitude across the sessions (VP2, VP3, VP4, VP5) between the two groups showed a significant effect of the session [$F(3,78) = 18.60$, $p < .001$] and a significant interaction between group and session [$F(3;78) = 3.16$, $p < .03$]. Post hoc comparisons showed a significant decrease of adaptation between VP2 and all the other sessions in both groups (all $ps < .03$). There was also a significant decrease of adaptation between VP3 and VP5 in the single-step group ($p < .05$),

Figure 5. Mean after-effects (\pm standard errors) are presented for all parameters in the multiple-step group (mul) and in the single-step group (sin), for right (r) and left (l) hands. Negative values correspond to leftward-pointing shifts. Parameters presented are visual pointing (VP) and auditory pointing (AP).



whereas there was no decrease in the multiple-step group from VP3 to VP5 ($p > .3$).

Robustness of Adaptation during VP5 Trials

During the VP4 session (as well as for all previous measurements), there was no modification of pointing behavior across trials. A repeated measures ANOVA comparing the variables across pointing trials showed no significant difference between the two groups [$F(1,11) = 0.45$, $p > .52$]. In VP5, however, there was a consistent trend in pointing errors over trials. In both groups, the amount of after-effect increased from the first pointing movement and then reached a plateau. The variable “VP5 – mean VP4” was calculated for each group as a measure of de-adaptation from the previous individual VP4 level. A Kolmogorov–Smirnov test was performed to ensure normality of the distribution of the variable (VP5 – mean VP4). The mean level of this variable was $-0.89^\circ \pm 0.11^\circ$, and the comparison of this variable to zero showed a significant difference [$t(11) = -7.81$, $p < .001$]. To sum-up, the robustness corresponds to the increasing of after-effects across trials in the VP5 session. This apparent strengthening of adaptation was again more obvious in the multiple-step group than in the single-step group. Furthermore, it was surprising that the after-effects increased across measurement trials in both groups.

DISCUSSION

It has been shown recently that neglect patients lack an awareness of the spatial distortion that occurs during prism adaptation, and that the patients exhibit greater and longer-lasting negative after-effects. The present study simulated neglect-like unawareness of optical deviation in healthy subjects by reducing the detection of the optical shift in one group (multiple-step group), and by making the introduction of the optical shift obvious in another (single-step group). The main findings reveal

that the multiple-step group showed: (1) larger after-effects in visual pointing with the adapted hand; (2) significant transfer to the nonexposed hand for both visual and auditory pointing tasks, and (3) greater robustness of adaptation following the de-adaptation trials. The increase of after-effects across trials during VP5 will be analyzed and discussed in more detail in a separate report.

The basic result of the present study is that unawareness favors the development of adaptation. The level of adaptation was 40% for the single-step group versus 56% for the multiple-step group, although the single-step group had 50% more trial-degrees of optical deviation than the multiple-step group. Our results clearly demonstrate that it is not simply the absolute quantity of exposure that is the main parameter of prism adaptation. Awareness of the optical shift plays a detrimental role in the adaptation processes. Although it has been shown that awareness of the sensorimotor conflict reduces the adaptation (e.g., Jakobson & Goodale, 1989), the classical conception of prism adaptation has consistently underlined the necessity of subjects producing errors during the first pointing trials in order that prism adaptation may develop (Redding & Wallace, 1992; Welch et al., 1974; Welch, 1971; Welch & Rhoades, 1969). However, two main arguments seem to invalidate this idea.

First, we have to consider the importance of the first pointing errors on after-effects. Removal of the prism after this first accurate pointing behavior would undoubtedly fail to reveal a negative after-effect of commensurate size. Therefore, strategic correction of pointing error during the error reduction period does not qualify as true adaptation (Welch & Goldstein, 1972). *Second*, it does not appear to be necessary for prism adaptation that subjects are aware of pointing errors. A first argument in this regard comes from the concurrent adaptation procedure with slow arm movements. In this situation, subjects typically reveal significant adaptation, whereas it is rare that they spontaneously report that anything seems to be wrong with their vision (Redding & Wallace, 1988).

A further argument concerns experimental procedures using small displacements which allow examination of the process of visuomotor realignment free of contamination by “conscious” correction (e.g., Jakobson & Goodale, 1989). Noteworthy, when Howard (1968) used small displacements such that the subjects never suspected the presence of visual shift (prismatic shaping procedure), the adaptation was substantial. The association of strong adaptive after-effects with unconscious perturbations is not restricted to prism adaptation. Indeed recent motor adaptation procedures using unconsciously perceived incremental steps have also induced large and robust pointing after-effects (Magescas & Prablanc, 2006).

It is extremely interesting to compare our results to a related experiment in which exposure was made multiple-step but where larger optical steps were introduced. Lazar and van Laer (1968) adapted three groups of subjects as follows: first with 6°, then 12°, and finally, 18° prisms (Group 1); first with 12°, and again 12°, and finally, 18° prisms (Group 2); or directly with 18° prisms (Group 3) for the same number of pointing trials during prism exposure. It should be remembered that a 6° shift is easily detected by healthy subjects (Jakobson & Goodale, 1989). The largest after-effects were observed in Group 3 and the least after-effects in Group 1. This may suggest that the level of adaptation may simply depend on the quantity of visual exposure, when subjects are made aware of the distortion by large steps. On the contrary, the reverse pattern of results was observed in our study probably because the development of prism adaptation occurred under the awareness threshold. It is of prime importance to underline here the fact that both the aware and unaware modes of prism exposure can give rise to adaptation. In the more classical aware mode (as in our single-step group), both strategies and realignment contribute to the error reduction. However, the stronger power of strategies to reduce pointing error in the short-term may reduce the error signals required for true adaptation (realignment) to develop.

The second part of the discussion deals with the robustness of after-effects. After-effects are known to decay with time (e.g., Foley & Maynes, 1969; Hamilton & Bossom, 1964; for review, see Welch, 1986). The present results strikingly showed that after performing the close-loop pointing task without prisms (de-adaptation), the magnitude of after-effects increased again across the trials of the latest after-effect measurement session (VP5), whereas no such trend was observed after the short period of rest in darkness (VP4). These results suggest that there was a difference in time course between the recalibration component involved in the closed-loop pointing session, and the preservation of the realignment component in the VP5 session. This interpretation was also suggested by Kravitz and Yaffe (1974). Furthermore, the present study showed that the simulation of neglect unawareness of optical shift in the multiple-step group

produced longer-lasting after-effects than the single-step group. Hence, it can be argued that awareness of the optical shift even plays a detrimental role upon the robustness of adaptation. Interestingly, this result is compatible with observations made in neglect patients (e.g. Rossetti et al., 1998).

The third section will briefly discuss the potential involvement of anatomical substrates of prism adaptation, and the contribution of our results to the understanding of realignment in neglect patients. The literature attributes a crucial involvement of the cerebellum in the adaptive realignment process because of its important role in the integration of motor and visual information (Pisella et al., 2005; Baizer, Kralj-Hans, & Glickstein, 1999; Thach, Goodkin, & Keating, 1992; Weiner et al., 1983; Held 1961; for review, see Jeannerod & Rossetti, 1993). The frontal cortex also appears to be involved in adaptation (Kurata & Hoshi, 1999; Canavan et al., 1990). The parietal cortex is involved both in strategic calibration (superior parietal cortex) (Pisella et al., 2004; Inoue et al., 1997; Clower et al., 1996; Meier, 1970) and in representational after-effects partly responsible for neglect rehabilitation by prisms (temporo-parieto-occipital junction) (Luauté, Michel, Rode, Pisella, et al., 2006; Pisella, Rode, Farnè, Tilikete, & Rosetti, 2006; Luauté, Michel, Rode, Boisson, et al., 2002). Neglect patients show an extraordinary level of adaptation to prisms, while also exhibiting a lack of awareness of the optical deviation (Rode et al., 2003; Rossetti & Rode, 2002). More recently, investigations using skin conductance recording showed that when large prismatic shifts were unexpectedly introduced in the course of a pointing task, neglect patients showed a reduced vegetative reaction as compared to healthy subjects or to right brain-damaged patients without neglect (Calabria et al., 2004). These and the present results lead us to conclude that unawareness of the optical exposure strengthens true adaptation, transfer, and robustness. Altogether, we wish to put forward the notion that there is a functional balance between the respective contributions of parietal (strategic recalibration) and cerebellar brain areas (adaptive realignment). When the strategic component is reduced either by cerebral damage or by manipulations such as those used here, the true adaptation appears to be reinforced. Cerebellar plasticity might be considered as being under parietal control. However, experimental reduction of awareness cannot entirely simulate the magnitude of adaptation seen in neglect patients. This raises the question of whether the adaptability of neglect patients may be due rather to cerebral plasticity or brain asymmetry following brain damage, than to the mere reduction of the strategic recalibration.

Neglect patients also show an extraordinary transfer to cognitive domains (e.g., Rossetti et al., 2004; Rode et al., 1998; for reviews, see Rode et al., 2003; Rossetti & Rode, 2002). The question remains open whether there is a proportional link between cognitive and sensori-

motor after-effects. Considering that in healthy subjects the classical procedure of prism adaptation is responsible for cognitive after-effects qualitatively similar to neglect symptoms (Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004; Berberovic, & Mattingley, 2003; Michel, Pisella, et al., 2003; Michel, Rossetti, Rode, & Tilikete, 2003; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000), it would be interesting in the future to investigate whether increasing the adaptive component would also increase neglect-like behavior (for review, see Michel, 2006).

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Reprint requests should be sent to Carine Michel, INSERM ERM 207, Motricité-Plasticité, Université de Bourgogne, BP 27877, F-21078 Dijon, France, or via e-mail: carine.michel@u-bourgogne.fr and Yves Rossetti, Espace et Action, UMR-S 534 INSERM - UCBL, 16 Avenue du Doyen Lépine, F-69676 Bron Cedex, France, or via e-mail: rossetti@lyon.inserm.fr.

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