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New Visuomotor Mappings of Wrist Rotations Are Ignored if Continuous Visual Feedback Is Available

Abstract

Mechanisms involved in the production of visually guided reaching movements have been extensively investigated, but little is known on the motor control of wrist rotation. In two independent experiments, we examined the adaptation of wrist motor control to new visuomotor gain in rotation in a task where subjects were asked to adjust the orientation of a virtual teapot using a force feedback robot arm without time constraints. We manipulated the visual feedback to assess how feedback affects the mechanisms employed by the motor system to compensate for the imposed visuomotor gain. In the first experiment, continuous visual feedback was provided to subjects during the learning phase with the new visuomotor gain. In a second experiment, which used a different design, only terminal feedback was provided, also as a visual teapot. We tested whether adaptation to yaw (flexion/extension) wrist rotations could transfer to pitch (ulnar/radial) rotations, as suggested by earlier work. We showed that in conditions close to robotic arm manipulations by teleoperators (when continuous visual feedback is available and the movement duration is not limited), novel visuomotor gains of wrist rotations are spontaneously taken into account without the need for adaptation. Nevertheless, an internal model of the new visuomotor gain was constructed in parallel, since limited, but significant, aftereffects were observed. For the second experiment, for which visual feedback was only provided after the manipulation, a clear adaptation with an internal model updating to new visuomotor gain was observed. This adaptation was transferrable to another wrist axis. However, after the transfer of the adaptation, subjects spontaneously and rapidly returned to a gain of 1.

1 Introduction

Adaptation to visuomotor perturbation was considered in the last century, as one of the most appropriate paradigms to investigate mechanisms involved in the production of visually guided reaching movements. Perturbation of visuomotor gain (i.e., variations of the relation between cursor motion and the associated hand movement) and visuomotor rotation (differences between the direction of cursor motion and the associated hand movement) in the horizontal plane were extensively used. Psychophysical studies have shown that the central nervous system plans the motor commands by independently processing amplitude and direction of the movement through feed-forward mechanisms

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(Bock, 1992; Gordon, Ghilardi, & Ghez, 1994; Rossetti, Desmurget, & Prablanc, 1995; Krakauer, 2009; Krakauer, Pine, Ghilardi, & Ghez, 2000; Vindras & Viviani, 2002). Changes in the motor commands that take the perturbation into account were interpreted as adaptation, that is, the updating or construction of internal models of new visuomotor mappings between the physical space where the motor action occurs and the visual screen showing the feedback (Kawato, 1999).

Earlier studies indicate that the type of visual feedback while training with a given perturbation of visuomotor coordination is an important factor for adaptation (Heuer & Hegele, 2008). Two types of visual feedback were classically used: continuous feedback of hand position that corresponded to closed-loop control; or posttrial visual feedback that corresponded to open-loop control (Jordan, 1996). Apparent contradictory results have been reported in the literature. On the one hand, some studies demonstrate that only continuous visual feedback can induce adaptation measured by postpractice aftereffects (Hinder, Treslian, Riek, & Carson, 2008; Liu & Scheidt, 2008; Flanagan & Rao, 1995; Goodbody & Wolpert, 1999). On the other hand, previous investigators claimed that adaptation is dependent on posttrial feedback (Heuer & Hegele, 2008; Bernier, Chua, & Franks, 2005). The nature and complexity of the visuomotor transformation as well as the degree of consciousness of the perturbation may be the key factors for these inconsistent results. In the case of visual closed-loop control, Smeets, Van den Dobbelsteen, De Grave, van Beers, and Brenner (2006) argue that accurate movements without access to an internal model are possible, because online visual control is sufficient to accurately perform the action. This hypothesis can only be investigated when the duration of the movement is not time-constrained. Indeed, a strong limitation of the movement duration may prevent the use of visual feedback for online corrections, thus requiring the construction and updating of internal models (Fernandes, Albert, & Kording, 2011; Fernandez-Ruiz, Wong, Armstrong, & Flanagan, 2011). The initial motivation of the present study was to improve knowledge on rotational control of teleoperators that use robotic arms. Since such operations do include continuous visual feedback and are not time-constrained, we used similar experimental conditions to those in our first study.

In contrast, in the case of open-loop control with terminal feedback, adaptation to the perturbation can only be obtained when a sufficient internal model of the perturbation has been built. Accordingly, Uhlarik and Canon (1971) showed that attention is focused on visual information during the execution of movements with continuous visual feedback, whereas attention is focused on kinesthetic information with terminal visual feedback. The type of visual feedback may not only have influence on the adaptation and on internal model construction of new visuomotor mappings; it can also affect the transfer of the visuomotor adaptation. It has been reported that subjects who adapt to a visual distortion using one arm subsequently show signs of adaptation when using the unpracticed arm (Choe & Welch, 1974; Imamizu & Shimojo, 1995; Sainburg & Wang, 2002). This transfer of adaptation has been proven to be modulated by the type of visual feedback. Indeed, Cohen (1967, 1974) showed that the manual adaptation of pointing to visual and auditory targets was transferred to the unexposed arm after practice with terminal visual feedback, but not after practice with continuous visual feedback.

In adaptation to visuomotor perturbation studies, the effect of visual feedback and the transfer of adaptation were mostly investigated for hand movements in the horizontal plane. To our knowledge, no study addressed the adaptation of wrist rotation to new visuomotor gains under conditions close to robotic arm manipulations by teleoperators (i.e., when continuous visual feedback is available and the movement duration is not limited). Only one recent study measured the generalization curves for visuomotor rotations applied to wrist movement (Fernandes et al., 2011). The authors reported that subjects readily learn a perturbation (rotation of 30° of cursor position during movements) and generalize locally, in a similar way to what was previously reported in reach adaptation studies. Interestingly, the wrist provides an appropriate model to study adaptation, since the wrist has 3-DOF rotation; thus, intrasegmental transfer of adaptation can naturally be investigated. Furthermore, unlike for horizontal arm movements in reaching tasks, wrist rotation limits the potential compli-

cations resulting from a high number of degrees of freedom available in such tasks. Moreover, it eliminates the effect of anisotropic viscous and inertial properties of the limb (Pellegrini & Flanders, 1996). Finally, with the increasing importance of virtual reality and development of technical tools such as robotic surgery, teleoperation, and virtual manipulation of objects, the investigation of wrist adaptation under conditions close to robotic arm manipulations by teleoperators appears essential.

The aim of the present study was twofold. We were interested in a first study in the adaptation of wrists to new visuomotor gains when continuous feedback was provided. We hypothesized that the learning in the presence of continuous visual feedback would result in efficient wrist manipulation but little adaptation once the visual feedback was suppressed. Indeed, we questioned whether a real construction of new visuomotor mappings or an internal model of the new gain could be achieved when the movement time is not limited. In a second independent experiment, we investigated the adaptation to new visuomotor gains when visual terminal feedback is provided. As already observed for arm movements in the horizontal plane, it was expected that visual terminal feedback would result in a clear adaptation. Accordingly, we designed experimental conditions that allowed the investigation of the transfer and the extinction of adaptation. Note that the design of the two studies was deliberately different and aimed at investigating different processes involved in the adaptation to a new visuomotor gain. Thus, both studies were not planned to be directly compared, but the theoretical implications put both experiments into perspective.

2 Experiment 1: Visuomotor Adaptation in Closed Loop

In the first experiment, we investigated the possible adaptation of wrist movement to new visuomotor gains when continuous visual feedback was available.

2.1 Methods

2.1.1 Subjects. Eleven volunteer subjects (6 men and 5 women, 26 ± 7 years old), naive to the goals and hypotheses of the experiment, participated in the study. All had normal or corrected-to-normal vision (subjects who wore glasses or contact lenses did so during the experiment), and none had any known visual, neurological, or oculomotor impairments. All subjects were right-handed (according to the Edinburgh protocol) and gave their informed consent in accordance with the local ethics committee guidelines.

2.1.2 Apparatus. Subjects stood upright, facing a 250 × 180 cm screen at about 120 cm distance from their eyes and were asked to match the orientation of a virtual teapot with a translucent version of the same object, the target teapot. The teapots were presented in the front projection screen at a virtual height of 1 m. The orientation of one of the teapots was controlled by the subjects with a force-feedback Virtuose robotic arm (6D35-45, http://www.inition.co.uk/inition/dispatcher.php?URL_=product_ffhaptic_haption&&model=products&action=get&tab=summary). The Virtuose robotic actuator was blocked in translation and could only be rotated about one of the three axes of rotation (yaw: flexion/extension; pitch: ulnar/radial deviation; and roll: pronation/supination) according to the experimental procedure. During the manipulation, the kinematic equation linking the teapot visual orientation angle $\theta(t)$ to the corresponding haptic orientation angle $\tau(t)$ is given by: $\theta(t) - \theta_{init} = \gamma.\tau(t)$, where γ is the visuomotor gain and θ_{init} is the initial visual angle. The constant visuomotor gain (γ) introduced between the teapot and the wrist rotation was also manipulated. In order to get a proportional increase of the visuomotor gain on a logarithmic scale, the following gain values were used: 1/2; 1; 2; and 4. Finally, three different values of expected haptic angle (θ_{init}) were used: 10°, 20°, and 30°. The initial angles were chosen within the limits of the robotic arm clearance that could not exceed ±45°. The direction of rotation (left/right for yaw, up/down for pitch, CW/CCW for roll) was counterbalanced. For each trial, rotations of the actuator were restricted to the axis of the tested condition: the robotic arm was programmed to block rotations about any other axis. In this project, the robotic arm was used for three purposes: to restrict the possible movements of the actu-

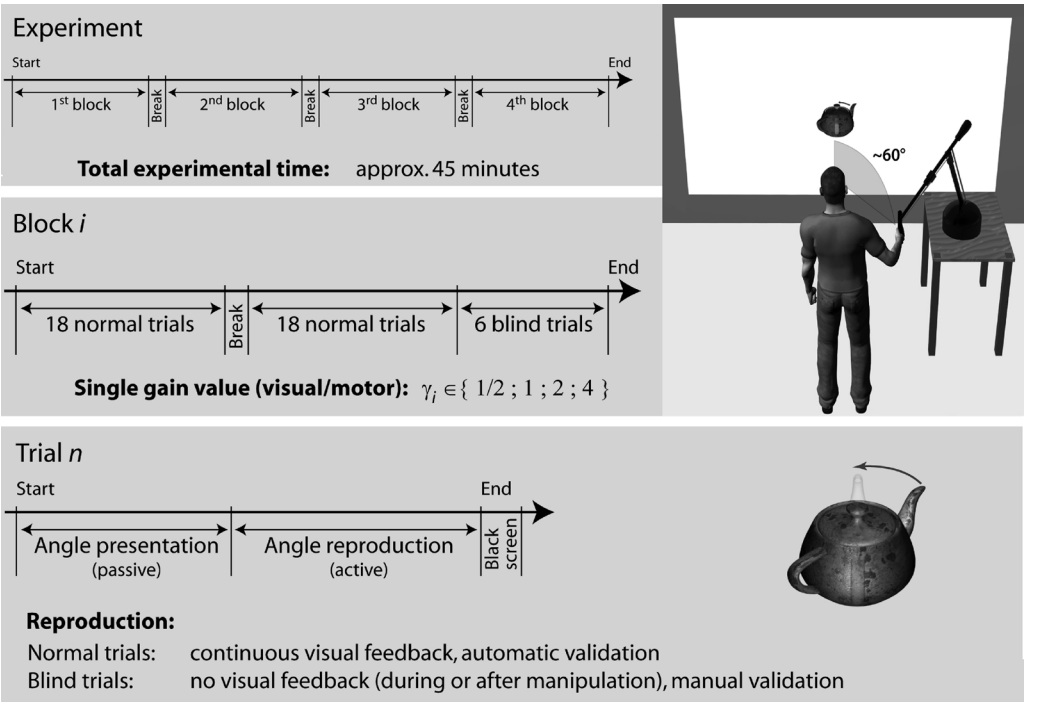


Figure 1. *Setup illustration and sequence of the phases of Experiment 1. The first line shows the sequence of the experiment, the next lines describe the timeline of a block and of a trial with an illustration of teapot stimuli (target and controlled teapots).*

ator to one axis of rotation; to automatically bring back the actuator and the hand of the subject to its initial position; and to measure the instantaneous speed and position of the actuator.

2.1.3 Design procedure. The timeline of the experiment is detailed in Figure 1. The experiment was composed of four successive blocks, one for each of the visuomotor gains investigated (1/2; 1; 2; 4). The block order was randomly defined for each subject. In each block, 36 trials with continuous visual feedback of the adjustments were used (learning phase), followed by six blind trials (adaptation test phase). The three axes of rotation tested (yaw, pitch, and roll) were counterbalanced within each block. In order to assess adaptation as would be observed in a standard teleoperation situation, we decided to mix within each block of trials all three axes of rotation in a random sequence. All trials started with the presentation of both objects for 500 ms, and the object controlled by the subject was then rotated to the initial visual angle. The initial visual angle was determined as a function of the gain and the expected haptic angle. For instance, an expected haptic angle of 10° corresponded to a 20° visual angle, for a gain of 2. The order of the initial angle was randomly defined for each block, and subjects were asked to adjust the controlled teapot in order to match the orientation as quickly as possible, although without a strict time limit, with the orientation of the target teapot (see Figure 1). In normal trials, continuous visual feedback was provided and the trial ended automatically when the subject's adjustment satisfied the validation criterion (see Figure 2). The criterion of the trial's end was achieved when the orientation of both teapots matched within a haptic tolerance range of $\pm 1^\circ$ (ε_{val} in Figure 2) for a minimum period of 500 ms (Δt_{val}). A green background was the feedback provided to the subjects when they entered the validation area for 200 ms. This delay was used in order to prevent any additional cues for the adjustments, in particular when crossing the expected haptic angle. (Note that this

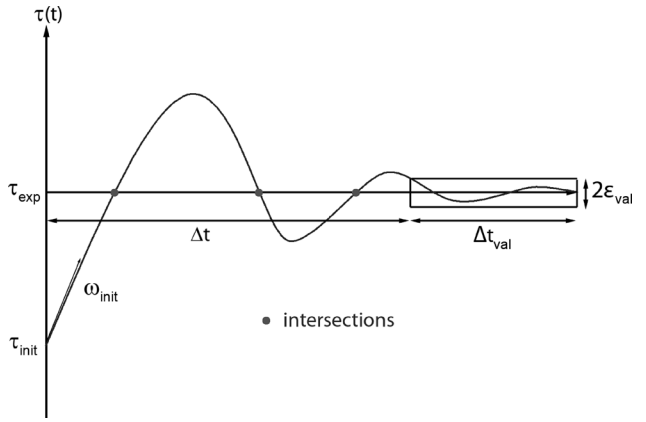


Figure 2. *Representation of schematic trial's curve τ(t) of robotic arm rotation across time. ω_{init}: initial haptic speed; τ_{init}: initial angle of the robotic arm; τ_{exp}: expected robotic arm position; t_{end}: manipulation latency; Δt: criterion of trial end (500 ms); 2ε: tolerance range of expected position.*

moment of crossing the expected haptic angle is shown in Figure 2 as the intersections of the oscillating curve with the expected angle, τ_{exp}.) At the end of the trial, the robotic actuator was automatically brought back to the starting position. In blind trials, there was no visual feedback during the manipulations; therefore, the validation was controlled by the subjects: they were instructed to press a button on the actuator once they were satisfied with their wrist rotation. A direct view of the hand was restricted, because the hand was at about 60° of visual angle from the center of the screen, where the resulting visual motion was displayed (see Figure 1). Furthermore, the instruction to perform the task as quickly as possible and the automatic return to the initial position of the robotic actuator at the end of each trial also limited the possibility of using visual feedback of the terminal hand position.

2.1.4 Data Analysis. For each trial, the orientation of the robotic actuator sampled at 85 Hz was recorded throughout the manipulation duration. In the learning phase (normal trials), this measure provided three indexes of the subject's wrist movement computed as follows (see Figure 2): the initial haptic speed corresponding to the initial slope ω_{init} of the curve $\tau(t)$; the manipulation duration (Δt) between the beginning of the wrist motor rotation and the beginning of the validation period; and the number of times that the curve $\tau(t)$ intercepted the expected haptic angle (τ_{exp}) during manipulation latency (Δt). In the adaptation test phase (blind trials), the dependent variable of interest was the used/trained gain ratio (in percentage). The percentage inferior/superior to 100% corresponded to a gain during the blind trials that was inferior/superior to the gain presented during the normal trials, respectively.

Analyses of variance (ANOVAs) were performed on all dependent variables with the visuomotor gain (1/2; 1; 2; 4) and the expected haptic angle (10°; 20°; 30°) as within-subjects factors. In order to determine whether the first trial of a block was significantly different from the average performance of that block, we carried out a second ANOVA with an addition trial factor (first trial vs. mean of the remaining trials). Post hoc comparisons were carried out using Tukey's Honestly Significant Difference (HSD). When needed, one sample *t*-test was used in order to compare results to a single value. The first level of significance for these tests was set at $\alpha = 0.05$.

2.2 Results and Discussion

2.2.1 Learning Phase. The results of the initial haptic speed are presented in Figure 3(a). There were no significant effects of the visuomotor gain, $F(3, 30) = 0.77$; $p = .52$, or of the initial angle, $F(2, 60) = 1.43$; $p = .26$, on the initial haptic speed. Furthermore, there was no interaction between the two factors, $F(6, 60) = 1.24$; $p = .30$.

The manipulation duration results are presented in Figure 3(b). The statistical analysis of the manipulation duration revealed a significant effect of the expected haptic angle, $F(2, 60) = 113.8$; $p < .001$. The durations increased with the expected haptic angle, because subjects naturally took longer to adjust their wrists to an expected angle of 30° than 20° or 10° (both $p < .001$). Furthermore, adjustments to an expected angle of 10° were faster than adjustments to 20°; $p < .01$. There was an effect of the visuomotor gain, $F(3, 30) = 4.40$; $p < .02$, but no interaction between visuomotor gains and expected haptic angles, $F(6, 60) = 0.39$; $p = .88$. The

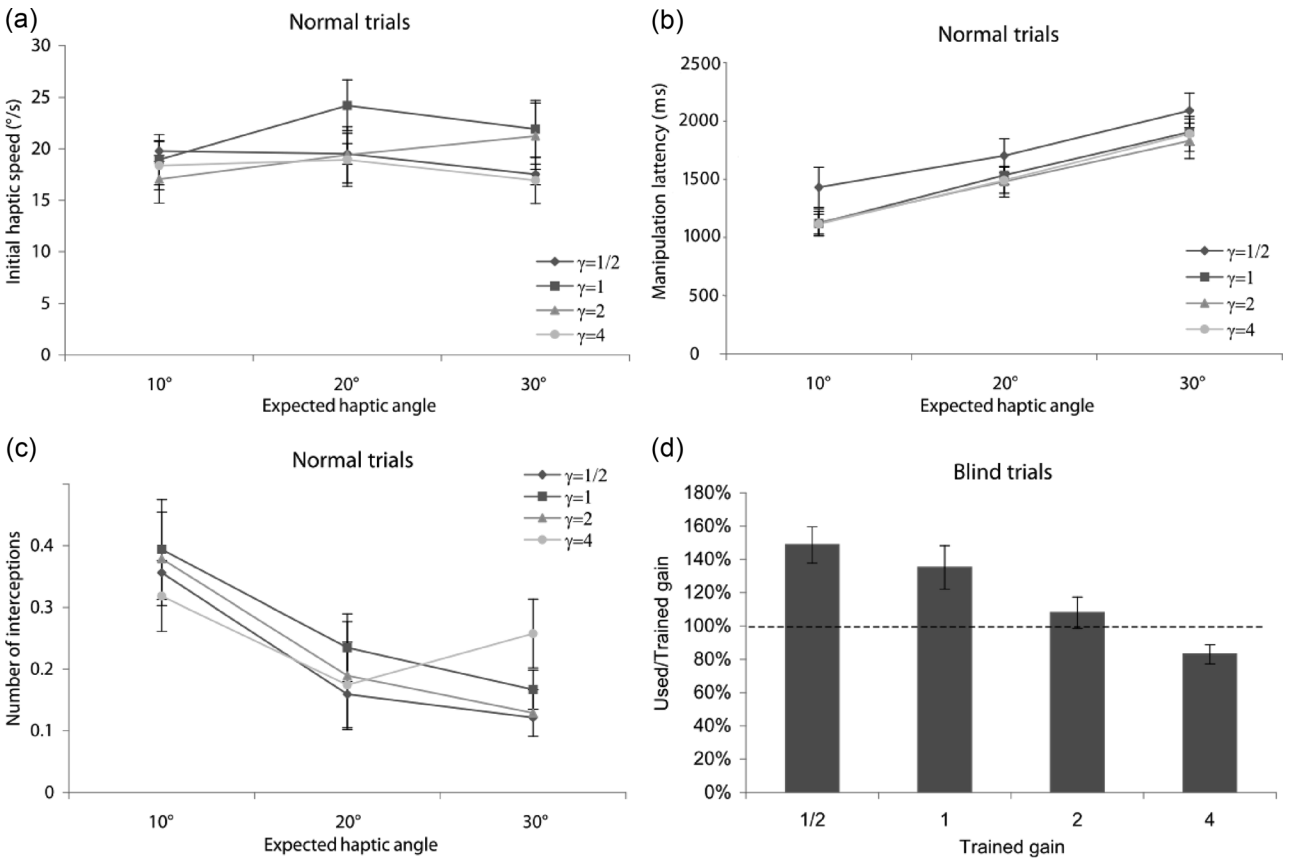


Figure 3. *Means over all trials for all subject and the three axis of (a) initial haptic speed, (b) manipulation latency, (c) number of interceptions, and (d) used/trained gain ratio (percentage) in blind trials as a function of the visuomotor γ gain (1/2; 1; 2; 4) and the expected haptic angle (10°; 20°; 30°). The error bars correspond to the standard errors of the mean.*

effect of visuomotor gain was due to the fact that the manipulations with a gain of 1/2 were slower than those with other gains: 1, $p > .05$; 2, $p < .02$; or 4, $p < .02$.

The results showing the number of times the subject's wrist angle crossed the target angle (τ_{exp}) are presented in Figure 3(c). The ANOVA performed on this number of interceptions revealed a significant effect of the expected angle, $F(2, 60) = 14.39$; $p < .001$. Indeed, the number of interceptions was greater for the 10° angles than both 20°; $p < .001$, and 30° angles; $p < .001$. Furthermore, the number of interceptions was not different for the 20° and 30° expected angles conditions; $p = 0.86$. There was neither an effect of visuomotor gain, $F(3, 30) = 0.63$; $p = .60$, nor an effect of interaction between visuomotor gain and expected haptic angle, $F(6, 60) = 1.18$; $p = .32$.

Furthermore, we found no significant main effect or any interaction whatsoever of the trial factor for any of the dependent measures (initial haptic speed, manipulation duration, number of interceptions), showing that the first trial did not differ significantly from the average of the remaining trials.

2.2.2 Adaptation Test Phase (Blind Trials). The results presented in Figure 3(d) indicate a significant main effects of visuomotor gain (1/2; 1; 2; 4), $F(3, 30) = 13.98$; $p < .0001$, on the used/trained gain ratio. The post hoc analysis of this effect revealed that used/trained gain ratios observed for trained gains of 1 and 1/2 were not different, $p = 0.23$, but both were larger than those observed with gains of 2, $p < .02$; $p < .0001$, and 4, $p < .0001$; $p < .0001$. One-sample t-tests

were used in order to compare the four used/trained gains ratios to the norm of 100%. These analyses revealed that trained gains of ½ and 1 induced larger ratios than 100%, $p < .0001$; $p < .02$, but smaller than 100% when the trained gain was 4, $p < .01$. In contrast, the ratio did not differ from 100% for a trained gain of 2.

2.2.3 Discussion. The results indicate on the one hand that training the participants with a given visuomotor gain does alter the performance between gains with continuous visual feedback. Indeed, during the learning phase, we found no anticipation—the initial haptic speed was identical whatever the gain of the trial was—and no increase of precision. Moreover, for each tested gain, we found that the same level of performance was achieved after the first trial of the associated block. This strongly suggests that when continuous visual feedback is available and the duration of the movement is not constrained, the mechanism underlying this visuomotor task does not require adaptation.

On the other hand, when the visual feedback was suppressed, there was a rather good correction for these new gains, although a global overestimation was found even for the gain of 1 (in blind trials). This suggests that for such a simple visuomotor task, an internal model of the new mapping is indeed constructed, although as long as the visual feedback remained available, an automatic and possibly generic dynamic control process takes place, which may not rely on internal models. Our results are consistent with the conclusions of Smeets et al. (2006) who demonstrated that online visual control is sufficient to accurately perform the action without access to an internal model. However, our findings also suggest that even if subjects used online visual corrections to reach the target, they may also have been adapted to the perturbation by a possible simultaneous construction of an internal model of the new mapping. Nevertheless, this adaptation was not optimal, since there was an overestimation of about 35% for the gains of 1/2 and 1, but an underestimation of 20% for the gain of 2. This result suggests that the online visual control could have slowed down the parallel adaptation, because it was sufficient to get a correct response. It can be postulated that increasing the number of trials would be sufficient to reach optimal adaptation in our experiment.

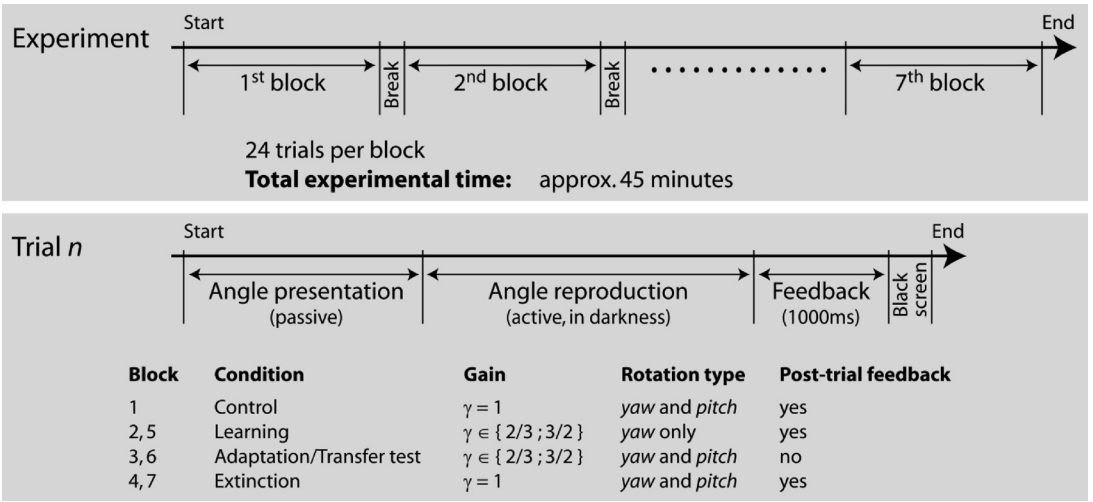
3 Experiment 2: Visuomotor Adaptation in Open Loop

In the second experiment, we opened the sensorimotor loop: there was no continuous visual feedback available during the manipulations (black screen). After practicing with the natural visuomotor gain of 1, subjects were asked to learn a new wrist visuomotor gain on the yaw (flexion/extension) axis with visual terminal feedback. The quality of adaptation for yaw rotations as well as the transfer of the adaptation to the pitch (ulnar/radial) rotations was then investigated in trials where the visual terminal feedback was no longer provided. Finally, the extinction of this adaptation was tested in trials with a gain of 1, as was done in the first control trials. The design of this second experiment was not comparable to the first one, including the gain values used for the adaptation.

3.1 Methods

3.1.1 Subjects. Twenty volunteer subjects (12 men and 8 women, 29 ± 6 years old), naive to the goals and hypotheses of the experiment, participated in the second experiment. The apparatus used was the same as in the first experiment.

3.1.2 Design Procedure. The aim of the second experiment was to investigate the learning, the adaptation/transfer, and the extinction of a new visuomotor gain (2/3 and 3/2) with only posttrial visual feedback (open loop). The gain values were selected in order to limit the possibility of the subjects becoming aware of the visuomotor gain perturbations. Indeed, if subjects became aware, explicit cognitive strategies could have influenced the responses and thus compromised the implicit adaptation interpretation. The experimental timeline is detailed in Figure 4. The experiment began with a control block that was used as the baseline performance with a gain of 1 for both the yaw and pitch axes (12 trials in yaw axis and 12 in pitch axis). Subjects



Block	Condition	Gain	Rotation type	Post-trial feedback
1	Control	$\gamma = 1$	*yaw* and *pitch*	yes
2, 5	Learning	$\gamma \in \{ 2/3 ; 3/2 \}$	*yaw* only	yes
3, 6	Adaptation/Transfer test	$\gamma \in \{ 2/3 ; 3/2 \}$	*yaw* and *pitch*	no
4, 7	Extinction	$\gamma = 1$	*yaw* and *pitch*	yes

Figure 4. *Sequence of phases of Experiment 2. The first line shows the sequence of the experiment and the second line describes the timeline of a trial. The yaw axis corresponds to the flexion/extension axis and pitch to ulnar/radial axis.*

had to match two visual object orientations as in Experiment 1, but in this experiment, only a terminal visual feedback of the adjustment was provided, and the screen remained black during the entire manipulation. The order of the trials was randomized. The next three blocks (2, 3, and 4) corresponded to the learning, adaptation/transfer, and extinction tests for one of the two new gains (2/3 and 3/2). The three last blocks (5, 6, and 7) corresponded to the similar investigation of the other new visuomotor gain. The order of presentation of the new gains was counterbalanced between subjects. Blocks 2 and 5 of the experiment corresponded to the leaning phase of each new visual gain (24 trials with visual terminal feedback), always in the yaw axis. The following blocks (3 and 6, respectively) corresponded to the adaptation and transfer test trials. In each trial of these blocks, after the presentation phase, the subjects were instructed to reorient the teapot without visual terminal feedback, either for the yaw axis (12 trials) or for the pitch axis (12 trials). The sequence of yaw and pitch trials was randomized. Since the new gains had only been learned on the yaw axis, in this block, the yaw axis manipulations allowed measuring the adaptation to the new visuomotor mapping, whereas pitch manipulations allowed testing of whether this learning transferred to pitch wrist rotations. Finally, the extinction of the learned visuomotor gain was investigated in blocks 4 and 7. In these blocks, the visuomotor gain was set back to 1 and subjects again had a visual terminal feedback. Three expected visual angles were used: 10°, 20°, and 30°; and the direction of rotation (left/right for yaw and up/down for pitch) was counterbalanced between trials. In all trials, subjects had to reorient the invisible teapot and validate the manipulation by pressing a button.

3.1.3 Data Analysis. For each trial, the orientation of the robotic arm after the subject's validation was recorded. A simulated gain was computed with these haptic manipulation values relative to the expected visual angles. The simulated gain was computed as the haptic manipulation angle divided by the visual angle value. In this second experiment, no continuous visual feedback during the manipulations was available. For each trial, the implicit gain used for the manipulation could be inferred from the final haptic angle. This design allowed measuring and analyzing the progression of the learned gain along the blocks.

Learning curves were fitted by means of nonlinear regressions performed on the simulated gain of the 24 learning trials (blocks 2 and 5) for both visuomotor gains (3/2 and 2/3). In order to analyze the adaptation/transfer and extinction data, a separate ANOVA

was performed with the trial sequence (initial sequence: trials 1–4; middle sequence: trials 5–8; final sequence: trials 9–12) and the test phase (control, adaptation/transfer, extinction) as within-subjects factors for each visuomotor gain (3/2 and 2/3) and for each axis of rotation (yaw and pitch). Furthermore, nonlinear regression analyses were performed on the data of the extinction phase. In addition, separate ANOVAs for 3/2 and 2/3 gains were performed on the simulated gain of the last six trials with the axis of rotation (yaw and pitch) and the phase (control, adaptation/transfer, extinction) as within-subjects factors. The nonlinear regressions were performed with SigmaPlot software. Post hoc comparisons were carried out using Tukey's HSD. The first level of significance for these tests was set at $\alpha = .05$.

3.2 Results and Discussion

Subjects were debriefed at the end of Experiment 2 in order to assess the participant's awareness of the perturbations. None of the participants reported having noticed a visuomotor gain modification, which validates the experimental design and the choice of the gains of 2/3 and 3/2.

3.2.1 Learning (Yaw Rotations). The results are presented in Figure 5. The nonlinear regression analysis revealed that an exponential increase to maximum function with three parameters fitted the data for 3/2 visuomotor gain learning, $f(t) = 1.16 + 0.3 \times 1 - \exp(-9.53 \times t)$; $R = 0.62$; $F(2, 23) = 6.48$; $p < .01$. Furthermore, an exponential decay function with three parameters fitted the 2/3 visuomotor gain learning, $f(t) = 0.73 + 0.25 \times \exp(-0.28 \times t)$; $R = 0.88$; $F(2, 23) = 36.9$; $p < .001$. The exponential constant (λ) of the fitting functions indicated a very fast learning speed of the 3/2 visuomotor gain, $\lambda = -9.53$, the latter being more than 30 times faster than for the 2/3 gain, $\gamma = -0.28$. In order to statistically test the learning speed (exponential constant), we computed for each subject: an exponential rise to maximum function for 3/2 gain and exponential decay for 2/3 gain. The individual exponential constant (λ) for 3/2 and 2/3 gains was compared with Student *t*-tests. This analysis statistically confirmed, $t(19) = 5.56$; $p < .0001$, that the gain of 3/2, $\lambda = -6.6 \pm 3.6$, was learned faster than the gain of 2/3, $\lambda = 1.3 \pm 3.3$.

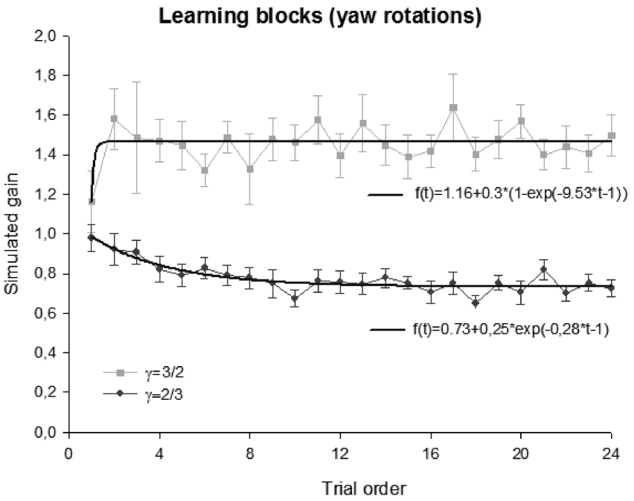


Figure 5. *Simulated gains on yaw axis as a function of the trial order for both experimental visuomotor γ gains (2/3; 3/2) during the learning phases. The error bars correspond to the standard error of the mean. Equations correspond to the best functions that fitted the data.*

3.2.2 Control, Adaptation and Extinction (Yaw Rotations). *3.2.2.1 Yaw Rotation, Gain 3/2.* The ANOVA with the trial sequence and the test's phases (control; adaptation; extinction), as within-subjects factors performed for the 3/2 visuomotor gain in yaw axis, revealed a main effect of the phase, $F(2, 38) = 46.41$; $p < .0001$ but neither trial sequence effect, $F(2, 38) = 1.73$; $p = .32$, nor interaction, $F(4, 76) = 0.04$; $p = .73$ were observed, as shown in Figure 6(a). The post hoc analysis of the phase effect showed that the simulated gain in the control and in the extinction phases were not different, $p = .999$, but both induced a lower simulated gain than the one observed in the adaptation test, both $p < .001$. Furthermore, the curves of simulated gain of the extinction trials were fitted with a nonlinear regression analysis. An exponential decay function with three parameters fitted the data, $f(t) = 1.07 + 0.35 \times \exp(-1.7 \times t)$; $R = 0.92$; $F(2, 11) = 26.8$; $p < .0001$. The extinction of the adaptation was 17 times less rapid than for the adaptation.

3.2.2.2 Yaw Rotations, Gain 2/3. The analysis of simulated gain on yaw axis after a 2/3 visuomotor gain

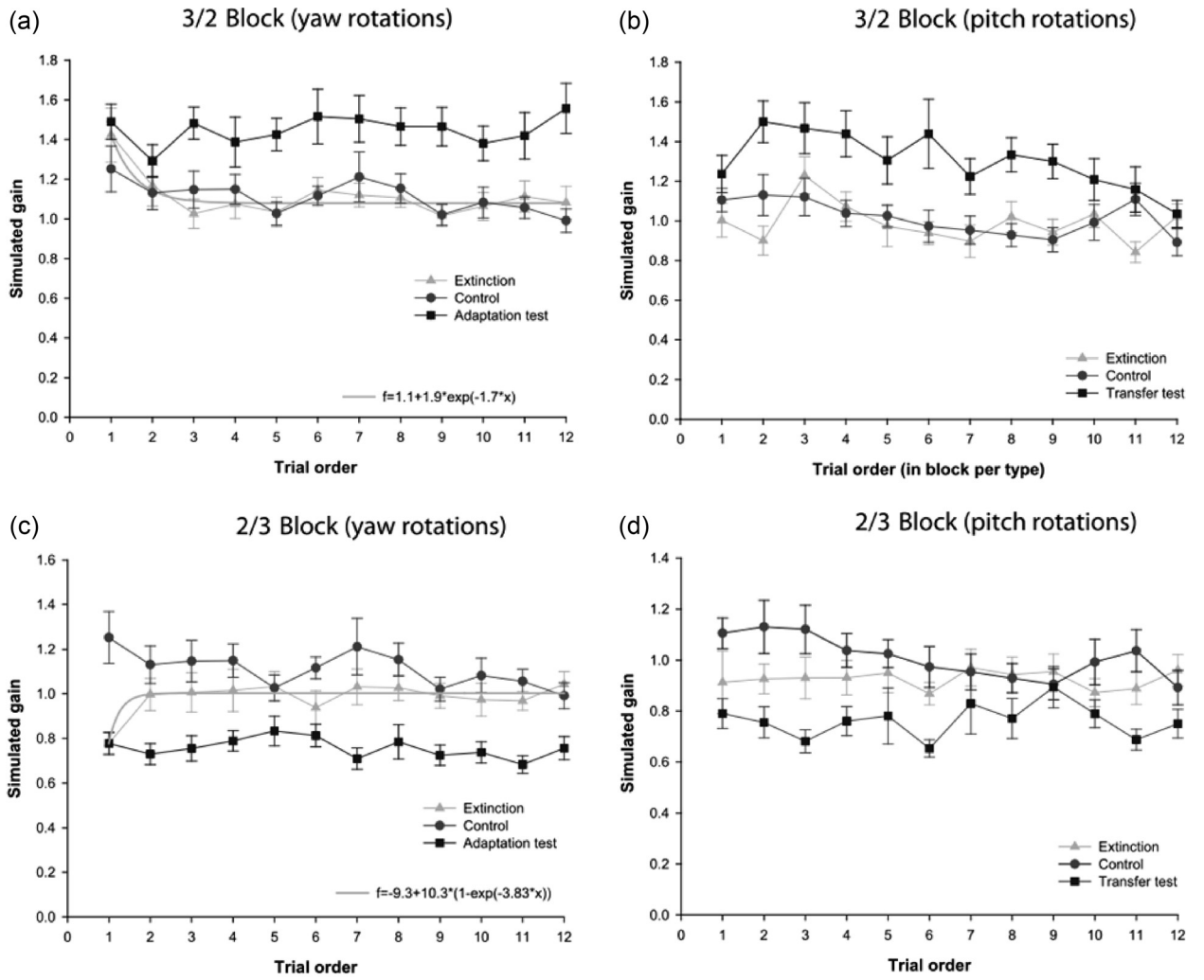


Figure 6. *Simulated gains in the three experimental phases (control, adaptation/transfer and extinction) as a function of the trial order on yaw (flexion/extension) and pitch (ulnar/radial) axis for (a, b) 3/2 and (c, d) 2/3 visuomotor gains. The error bars correspond to the standard errors of the mean. The equations correspond to the functions that fitted the extinction data.*

showed a main effect of the phase, $F(2, 38) = 53.7$; $p < .0001$, but neither trial sequence effect, $F(2, 38) = 2.13$; $p = .13$, nor interaction, $F(4, 76) = 2.37$; $p = .06$, were observed, as shown in Figure 6(b). The simulated gains observed, in the different conditions (control, adaptation, and extinction) were all different, all $p < 0.001$. Furthermore, a nonlinear regression analysis was performed on simulated gains of the extinction trials. This analysis revealed that an exponential rise function with three parameters fitted the data, $R = 0.9$; $f(t) = 0.77 + 0.22 \times (1–\exp(–3.83 \times t))$; $F(2, 11) = 19.8$; $p < .0001$. The extinction of the adaptation was 13 times more rapid than for the adaptation. Furthermore, the extinction of the adaptation to a 3/2 visuomotor gain was about half as rapid than for a 2/3 visuomotor gain.

3.2.3 Control, Transfer, and Extinction (Pitch Rotations). *3.2.3.1 Pitch Rotations, Gain 3/2.* The statistical analysis of the simulated gains revealed a main effect of both phase, $F(2, 38) = 21.49$; $p < .0001$ and trial sequence factors, $F(2, 38) = 11.34$; $p < .001$, but no interaction, $F(4, 76) = 1.20$; $p = .38$, as shown in Figure

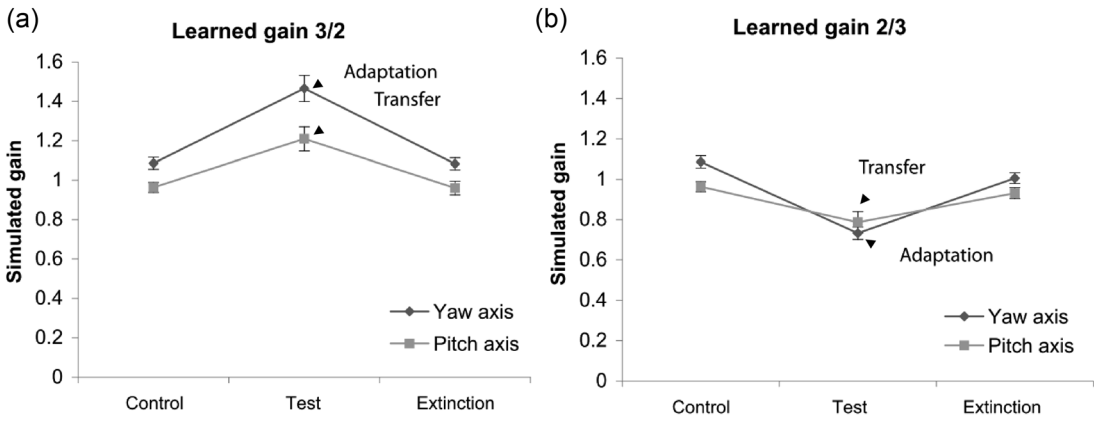


Figure 7. *Means of simulated gains of the three experimental phases (control, adaptation/transfer, and extinction) on both yaw (flexion/extension) and pitch (ulnar/radial) axis for (a) 3/2 and (b) 2/3 visuomotor gains.*

6(c). Decomposition of the phase effect showed that the simulated gain in the control and in the extinction phases were not different, $p = .91$, but both induced a lower simulated gain than the one observed in the transfer test, both $p < .001$. The post hoc analysis of the trial's sequence effect revealed that the initial sequence differed from the middle and the final sequence, both $p < .01$, while the middle and the final sequence were not different, $p = .31$. In this condition (pitch rotation; 2/3 visuomotor gain), nonlinear regression on the extinction data did not converge to a solution. A visual analysis of the data clearly shows that before the end of the transfer test phase, subjects had spontaneously returned to a gain of 1, which resulted in the extinction of adaptation before the first trial of the extinction phase.

3.2.3.2 Pitch Rotations, Gain 2/3. The ANOVA with the trials' order and the test's phases (control, transfer, extinction) as within-subjects factors performed for the 2/3 visuomotor gain in the pitch axis revealed a main effect of the phase, $F(2, 38) = 27.41$; $p < .0001$, but neither sequence effect, $F(2, 38) = 0.44$; $p = .64$, nor interaction, $F(4, 76) = 2.33$; $p = .06$, were observed, as shown in Figure 6(d). Post hoc analysis showed that the simulated gain measured in the control and extinction conditions did not differ, $p = .13$, but both were higher than the ones observed in the transfer condition, both $p < .001$. As already observed for the transfer of 3/2 visuomotor gain adaptation, transfer of the 2/3 gain spontaneously reduced during the transfer test phase leading to a manipulation gain close to 1 since the first trial of the extinction phase.

3.2.4 Control, Adaptation, Transfer, and Extinction According to the Axis of Rotation (Final Six Trials). *3.2.4.1 Visuomotor Gain of 3/2.* An ANOVA with the test phase (control, adaptation/transfer, and extinction) and axis of rotation (yaw, pitch) as within-subjects factors was performed on the simulated gains after learning the 3/2 visuomotor gain. This analysis showed the main effects of the test's phases, $F(2, 38) = 22.81$; $p < .001$, and axis of rotation, $F(1, 19) = 30.04$; $p > .001$. The interaction between these two factors was only marginally significant, $F(2, 38) = 2.94$; $p < .07$, as shown in Figure 7(a). The simulated gain was higher in the adaptation/transfer condition than in control, $p < .001$, and in extinction conditions, $p < .001$, but there was no difference between simulated gains of control and extinction conditions, $p = 0.99$.

3.2.4.2 Visuomotor Gain of 2/3. The ANOVA performed on simulated gain after learning the 2/3 visuomotor gain revealed a main effect of the test's phases, $F(2, 38) = 44.59$; $p < .001$, and of axis of rotation, $F(1, 19) = 4.2$; $p < .05$, as shown in Figure 7(b) . Furthermore, there was an interaction between these two factors, $F(2, 38) = 6.35$; $p < .004$. The analysis of the interaction showed that on both axes of rotation, the

simulated gain was not different in the control and extinction tests, on pitch axis: $p = .30$, and on yaw axis: $p = .95$; but these two conditions induced lower simulated gain than the adaptation/transfer condition, all $p < .05$. Furthermore, the simulated gain was neither statistically different on yaw and pitch manipulations in the adaptation/transfer condition, $p = .66$, nor in the extinction condition, $p = .34$. However, in the control condition, the simulated gain observed on the yaw axis was higher than the one observed in pitch axis, $p < .05$.

3.2.5 Discussion. These findings showed that it is possible to construct an internal model with only visual terminal feedback. The resulting visuomotor adaptation transfers to some extent to another type of rotation (from yaw to pitch). The induced gain for pitch rotations was partially but significantly updated, although contrary to yaw adaptation gain, this transferred gain decayed rapidly, suggesting the cancellation of the new mapping. These results may be explained by the nature of the axis used. Indeed, yaw rotations are very natural and benefit from a large range of motion; but pitch rotations are less intuitive. Participants may be less precise and less trained to perform target-matching tasks on this axis of the wrist, which could be a reason for the return to a gain of 1 after a few trials of the transfer block. It would be interesting to test in follow-up studies whether the same effect is observed when the axis of learning and transfer are swapped: that is, if the participant were trained on the pitch axis and the transfer tested on the yaw axis.

4 General Discussion

The nature of the visual feedback provided during the learning of a new visuomotor gain is known to influence the adaptation during hand movements (Shabbott & Sainburg, 2010; Veyrat-Masson, Brière, & Proteau, 2010). Nevertheless, the properties of wrist adaptation to a new visuomotor gain have never been investigated, to our knowledge, while it provides an appropriate model to study adaptation. Thus, we studied in two independent experiments the effect of visual feedback on wrist adaptation to a new visuomotor gain. In our first experiment, subjects practiced four new visuomotor gains on the three wrist canonical axes of rotation with a continuous visual feedback and without time constraints. The results demonstrated that performances were accurate in practice trials (number of interceptions, manipulation latencies) as if the subjects did not need to be adapted to the new visuomotor gain but spontaneously dealt with the perturbation. These results suggest the utilization of online correction from visual information and is matched by the results observed on the three variables used during practice (initial haptic speed, manipulation latency, and interceptions) since the participants' performance observed in the first trial of each block was not different from that of the following ones. Furthermore, the initial manipulation speed was identical, whatever the gain of the trial was. As there was no time constraint on the reaching task in the first experiment, it is likely that subjects always started the task with a similar short movement and then relied on the visual feedback to correct online for the visual perturbation. Consequently, in Experiment 1 the wrist movement might not rely on feedforward control. This interpretation of the results is in line with previous studies involving arm movements (Saunders & Knill, 2003; Smeets et al. 2006) however it has been suggested that an internal model of the perturbation can be created with continuous visual feedback when the manipulation duration is limited (Fernandes et al., 2011; Fernandez-Ruiz et al., 2011; Hinder et al., 2008). A limitation of the movement duration may prevent the use of visual feedback for online corrections, thus requiring the construction and updating of internal models. It can be suggested that a strictly constrained movement's time may have induced bigger adaptation effects and possible differences in initial haptic speed. However, the analysis of the initial haptic speed also revealed that the subjects did not anticipate the different angles, suggesting that the initial haptic speed is not a very sensitive measure of anticipation. Finally, we observed aftereffects in the blind trials that followed and where visual feedback was suppressed. This result indicates that participants were adapted to some extent to the new visuomotor gain. If performance observed when continuous visual feedback was provided were based only on online correction, no post effect would

have been observed in the blind trials without the visual information that followed.

Taken together, the results of Experiment 1 indicate that for visuomotor reaching tasks involving wrist rotations with different gains but without time constraints, subjects perform accurately, probably through online visual corrections. An automatic and rather implicit correction of the visuomotor coordination seems to occur, as visual guidance of the wrist proved to be sufficient for a correct movement whatever the gain was. Despite this very efficient online correction, an adaptation (aftereffect) was observed when the visual feedback was suppressed, suggesting that an internal model of this gain might be built in parallel but not used.

In the second experiment, the sensorimotor loop was opened, since no continuous visual feedback was given during the manipulations. Only posttrial visual feedback was provided. After practicing with the natural visuomotor gain of 1, subjects were asked to learn a new wrist visuomotor gain on the yaw axis with visual terminal feedback. The quality of adaptation for yaw rotations as well as its transfer to the pitch rotations was investigated in trials where the visual terminal feedback was no longer provided. Finally, the extinction of this adaptation was tested in trials with a gain of 1, as in the first control trials of the experiment. The results observed during the learning phase demonstrated that subjects acquired the new visuomotor gains very rapidly, leading to accurate manipulations after only a few trials. Nevertheless, we observed a strong difference in the learning speed for gains of 2/3 and 3/2. While adaptation to a gain of 3/2 was extremely fast and could be observed after only one trial, the adaptation to the 2/3 required approximately six trials. Furthermore, we observed during the adaptation tests that subjects were adapted to the new visuomotor gain and maintained it throughout the 12 trials without feedback. These results indicated that after practice of a new visuomotor gain with visual terminal feedback, subjects may have updated or constructed an internal model of the perturbation. The analysis of the last six trials of the adaptation/transfer phase indicated that the adaptation could be transferred from the learned axis of rotation (yaw) to another axis (pitch). Furthermore, we showed that the transfer of adaptation declined spontaneously across time, leading to the extinction of the adaptation after 12 blind trials. The decline of the transfer of adaptation corresponded to a return to a gain of 1 for both learned gains (3/2 and 2/3). When subjects learned the gain of 3/2, the transfer of the adaptation progressively decayed with a slow decrease of the produced gain to 1. When subjects learned the gain of 2/3, the gain progressively increased to 1. These results indicate that a learned gain on one axis of rotation could be transferred to another axis, but that some reinforcements are needed to maintain the transferred adaptation. Furthermore, after the transfer of adaptation, subjects spontaneously returned to a gain of 1, suggesting that the natural gain used by the subjects is 1. Unlike the transferred adaptation, the extinction of the adaptation on the learned axis was not spontaneous, but was induced by exposure to a visuomotor gain set back to 1. In this condition, both 2/3 and 3/2 adaptations extinguished very rapidly (nearly immediately). On the one hand the very rapid learning of the 3/2 gain extinguished rapidly and on the other hand, the 2/3 gain learning was slower but also extinguished rapidly. To our knowledge, the considerable asymmetry in the learning speeds of gains 2/3 and 3/2 was not reported in previous studies. It can be postulated that the difference of adaptation speed is linked to the existence of dual adaptation (Welch, Bridgeman, Anand, & Browman, 1993; Woolley, Tresilian, Carson, & Riek, 2007) for gains greater than 1 but not for those less than 1. Indeed, the very fast adaptation to the new gain greater than 1 could be due to the fact that in daily life subjects had previously been adapted to gains greater than 1 as, for instance, when using a computer mouse, a touchpad, or the steering wheel of a car. The rapid extinction (back to a gain of 1) after the adaptation to a novel gain (2/3 or 3/2) matched the hypothesis of dual adaptations to various gains (Welch et al.; Woolley et al.), since the novel gains may have been adapted concurrently with that of 1.

The nature of the visual feedback was found to have a strong effect on the way in which adaptation occurred. We showed that a clear adaptation with internal model updating to a new wrist's visuomotor gain and its generalization was clearly induced when visual feedback was provided after the manipulations. These results are con-

sistent with the observations of Heuer and Hegele (2008) that revealed adaptive shifts of movement amplitudes and aftereffects only with visual open-loop practices. Nevertheless, Hinder et al. (2008) showed that the adaptation of the production of isometric elbow torques to move a cursor toward visual targets after 60° rotation was dependent on continuous visual feedback. Liu and Scheidt (2008) also showed that spatial learning and generalization of novel finger coordination patterns required dynamic feedback of object motion in response to control signal changes; static information regarding geometric relationships between controller and endpoint configurations were not sufficient for generalization. These contradictory results may be explained by the fact that the type of transformation employed in our experiment (visuomotor gain modifications on one axis of rotation) is simplest to detect and to adapt online compared to classical visuomotor perturbations of reaching movements. Indeed, the perturbation gain employed in our study concerned the rotations on one axis (1 DOF) while in other studies, the gain affected movements of the arm in 2 or 3 dimensions. It may be postulated that when the visuomotor perturbation is complex, implicit and automatic adaptation observed with continuous visual feedback leads to a remapping of the visuomotor commands. In contrast, when the perturbation is less complex, the manipulation involves implicit and automatic processes that are visually guided and that do not require a remapping of visuomotor coordination. In these kinds of tasks, only visual feedback provided after manipulation allowed ensuring that an internal model of the new visuomotor mapping is created, which resulted in the observation of adaptation behavior with its classical characteristics, such as adaptation transfer and extinction. Alternatively, it can be postulated that wrist adaptation to new visuomotor gains present different properties compared to the hands or arms, since it involves rotations with limited clearance but no translation.

5 Conclusion

In conclusion, internal models of new visuomotor mappings can be acquired both with closed- and open-loop manipulations. However, when continuous visual feedback is available and the movement's duration is not constrained, the control of the movement may rely on visual feedback to correct online for the visual perturbation rather than on the internal models under construction. Our results revealed some properties of adaptation which are specific to wrist rotational control when the movement is not time constrained.

The initial motivation for this work was to improve knowledge on rotational control of teleoperators that use robotic arms. The findings reported here allow better understanding the role of visual feedback on the learning and usage of new rotational gains. The key application of our work lies in the human capacity to use rotational gains without prior learning provided that continuous visual feedback is available and time of movement not limited. This technique could be used to overcome the usual limitations of robotic arms in rotational control (range of about 40° for the Virtuose). The use of gains greater than 1 could replace the classical solution of unclamping/repositioning/clamping the actuator to the manipulated object, whether virtual or real, several times when performing large rotations. Follow-up studies could investigate how this capacity generalizes to the more useful unconstrained rotations by applying the gain around the instantaneous axis of rotation. Finally, the modifications of the visuomotor gain could be done online as a function of instantaneous haptic speed, in order to produce gains less than 1 for slower rotations (enhanced precision) and gains greater than 1 for faster rotations (efficiency for large movements). An important example of an application of this research is robotic surgery, where precision as well as efficacy for large rotations is crucial.

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