

Adaptation to a Visuomotor Shift Depends on the Starting Posture

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Baraduc, Pierre and Daniel M. Wolpert. Adaptation to a visuomotor shift depends on the starting posture. *J Neurophysiol* 88: 973–981, 2002; 10.1152/jn.00001.2002. Previous studies have shown that human subjects can adapt to a new visuomotor relationship that depends on the trajectory of the arm. However, these studies have not distinguished between hand- and joint-based learning models. We have examined whether different endpoint kinematics are necessary to obtain a differential visuomotor shift. The joint trajectory was varied by changing the initial posture, while maintaining a similar finger trajectory. After learning, maximum after-effects were found when movement began with the posture used during exposure to the visuomotor shift and decreased with the difference between initial and trained posture. This was shown to be independent of the final posture attained. Our results show that adaptation to a visual remapping cannot be due to the recoding of a desired final posture and depends on the arm trajectory in joint space.

INTRODUCTION

When reaching toward objects in our environment, we combine visual information of the position of the target and limb with proprioceptive¹ information to produce a correct motor command (e.g. Jeannerod 1988). The relationship between the incoming visual and proprioceptive signals evolve during the development of the individual and remain flexible in the adult: for instance, people who are used to wearing corrective glasses are able to adapt instantly to the distortions of the visual field that occur when they put their glasses on. Such distortions introduce a novel visual reafference associated with limb movements. Examinations of adaptation to such visuo-motor rearrangements have shed light on the neural processes involved in sensorimotor coordination (Weiss 1941). In particular, the way learning generalizes to novel situations can reveal the underlying computational structure of the adaptive process and help to constrain neuronal models.

To understand adaptation to novel visuomotor relationships, different modifications of the visual feedback have been used. These can either be implemented using optical devices, for example to induce a rotation of the visual field around the eye (Brown 1928; Ebenholtz 1966; Helmholtz 1925; Kohler 1955), or using virtual reality environments (Ghahramani and Wolpert 1997; Vetter and Wolpert 2000), in which arbitrary relation-

ships can be implemented. The largest body of data has been obtained using prismatic goggles, which essentially rotate the visual world about the eye. When subjects were required to wear these goggles, they readily adapted to the prismatic perturbation. This adaptation has been shown to involve separately or in combination a change in the perceived gaze position (perception of eye or head position), a change in felt arm position, and a change in the motor commands (sometimes called an “assimilated corrective response”), (Welch et al. 1974). Thus prism adaptation involves both a proprioceptive recalibration and motor or visuomotor learning (for reviews, see Harris 1965; Welch 1985).

More recent studies have revealed that prism adaptation can be restricted to specific arm kinematics or dynamics. For example, adaptation while throwing balls does not transfer from an overhand to an underhand throw (Martin et al. 1996). Similarly, learning to catch falling balls while wearing prism does not generalize to markedly different catching movements (Field et al. 1999). Prism adaptation during slow movements does not generalize to fast movements and vice-versa (Kitazawa et al. 1997). These results imply that adaptation cannot be simply a realignment of visual and limb-centered frames of reference.

However, in these studies, it is not possible to distinguish between hand- and joint-based learning models. In the studies of throwing and catching, the lack of generalization could be due to novel hand or limb configurations. Differential generalization depending on movement speed could be due to new temporal profiles of the hand position or joint angles. Therefore, it is unknown whether trajectory-specific adaptation is due to the different kinematics of the controlled endpoint or of the whole arm. To examine this issue, we have studied generalization of visuomotor learning when the joint trajectory is varied but the hand path is fixed.

Subjects were required to produce a pointing movement with the tip of the finger between a fixed starting point and target. The arm posture at the start of the movement was controlled by having the subjects match a specific arm orientation. Three initial postures were used, differing by the degree of humeral abduction. A visuomotor shift was introduced for a given initial posture, and its generalization to the other initial postures was tested. This procedure revealed a clear generalization gradient. The mechanisms responsible for this limb-configura-

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¹We here refer to proprioception as the sensory information conveyed by the whole set of muscle, tendon, joint, and skin receptors that allow the central nervous system to know the kinematic and dynamic state of the limb (Bosco and Poppele 2001).

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tion dependent adaptation were subsequently investigated through the analysis of the pointing kinematics.

METHODS

In two experiments described here, subjects were required to point to visual targets presented in a virtual-reality environment. The position of their finger could also be displayed online, and a computer-controlled discrepancy introduced between the actual and visually perceived finger location. We examined how learning such a visuomotor rearrangement generalized to novel arm configurations.

Subjects

EXPERIMENT 1. Eight right-handed subjects (3 men; 5 women; ages 21–33) volunteered to participate in the study.

EXPERIMENT 2. Ten right-handed subjects (4 men; 6 women; ages 20–32) volunteered.

Subjects had no history of neurological disorders and had normal or corrected-to-normal vision. They all gave their informed consent and were naive to the purpose of the experiment.

Apparatus and task procedures

The subjects' visual scene was the projection of computer-generated images of both the target and the visual feedback corresponding to the finger (Fig. 1). Stereo vision was achieved using alternating shutter glasses that ensured each eye only saw the appropriate left or right visual image (at 50-Hz frequency). Subjects therefore viewed a three-dimensional scene overlaid on their reaching workspace (for a full description of the virtual reality system and the calibration procedures, see Goodbody and Wolpert 1998). Subjects had their head supported by a chin rest, and glasses were fixed on the setup frame so that head movement was minimal. A splint was used to immobilize their right wrist and extended index finger, reducing the degrees of freedom of the arm to five (3 at the shoulder and 2 at the elbow).

The subject's arm position was recorded online with an Optotrak 3020 motion-analysis system (Northern Digital, Waterloo, Ontario) at 50 Hz. Twenty-three infrared-emitting diodes (IREDS) were mounted on three rigid bodies (RB) placed on the subject's right fingertip (8),

forearm (6), and upper arm (4), and left fingertip (5). The RB positions were used online to determine the visually displayed finger position (Procrustes analysis) (Schonemann 1966).

EXPERIMENT 1. In the first experiment, subjects learned a novel visuomotor rearrangement when pointing with the right hand to a target from a specified arm posture (the "trained posture"). After learning, the aftereffects were assessed for this trained posture as well as two other initial postures. The shoulder and finger positions being fixed at the start of the movement, the initial postures could differ by only 1 df, the abduction angle of the shoulder-elbow-finger plane. The three starting postures were defined for each subject in the following way: *posture 1* was defined as the most adducted posture the subject could adopt when maintaining his finger on the starting position. *Posture 2* and 3 were derived from *posture 1* by, respectively, a 30° and 60° rotation of the arm around the shoulder-finger axis.

To control the initial posture, subjects had to adjust their arm posture to align a blue cylinder oriented along their forearm with a green cylinder aligned with the initial desired orientation. To control the finger position, the distal end of the cylinders were displayed respectively at the tip of the index finger (blue) and the starting position (green). The coordinates of the starting point were $P_{\text{start}} = (0, 20, -42)$, the origin being set between the eyes (axes defined on Fig. 1, distances in cm). Each trial began when both the distance between the subject's finger and the starting position was less than 7 mm and the discrepancy between forearm orientation and starting orientation was less than 10°. This tolerance was necessary for the subjects to easily accomplish the task.

At the start of each trial the cylinders were extinguished and a 7-mm-radius green spherical target appeared 15 cm away from the starting location [$P_{\text{target}} = P_{\text{start}} + (0, 15, 0)$]. Subjects were required to place their index finger on the target. During visual feedback trials, the fingertip was displayed as a 7-mm-radius blue sphere. During no-visual-feedback trials, the finger position was never displayed. For visual-feedback movements, touching the target (distance between target and displayed position of finger less than 7 mm) was signaled by a beep and the target turning red. For all trials, the target disappeared at the end of the movement (when finger velocity went under 2 cm/s, after having exceeded 20 cm/s), and the visual feedback of finger position (when available) was extinguished until the subject's finger was brought back behind the frontal plane 5 cm in front (*y* axis) of the starting position. This initiated a new trial cycle. Trials with the left hand were without visual feedback and identical to those with the right hand except that no particular initial posture was required.

Each experimental session was divided in four phases: familiarization, pre-test, exposure, and posttest interspersed with rest periods. In the familiarization phase (approximately 20 trials), subjects pointed to the target under full visual feedback from all three initial postures.

The pre-test phase (80 trials) consisted in 24 blocks of three right-hand trials, interspersed with eight left-hand trials. Within each block of three there was a movement without visual feedback and two movements with visual feedback. All movements with visual feedback started from *posture 1*. The movements without visual feedback started from one of the three postures selected in pseudorandom order. Overall from each starting posture, subjects pointed eight times to the target without visual feedback. After every three blocks, a trial was performed with the left hand without visual feedback.

During the exposure phase (40 trials), the subjects repeatedly pointed to the target from posture 1 with the right hand. During these movements, visual feedback was always present, but a discrepancy between actual finger position and the visual feedback of finger position was introduced. The perturbation was introduced progressively over the first 20 trials. Specifically, the visual feedback of finger position was translated (from its true position) along the negative *x* axis in proportion to the sagittal distance the finger had traveled from the starting position ($y - y_{\text{start}}$). The discrepancy in the last 20 exposure trials was 0.67 cm for each centimeter moved along the *y* axis,

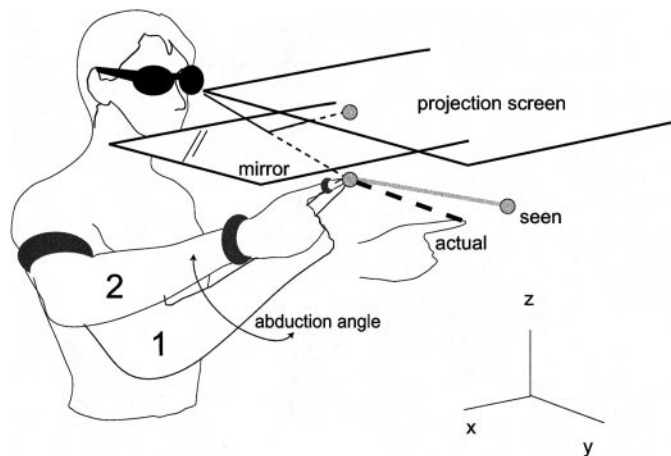


FIG. 1. Experimental setup. Arm position was recorded with infrared markers placed on the upper arm, forearm, and left and right index fingers. Computer-generated images were projected on a screen and viewed through a semi-silvered mirror. Shutter glasses synchronized to the graphics card allowed stereo vision. Subjects were required to adopt a specific initial arm posture at the start of the movement. *Postures 1* and 2 are shown. When movement started from *posture 1*, a visuomotor discrepancy was introduced, so that apparent movement direction (gray line) was rotated with respect to the actual direction (dashed line).

producing a 10-cm discrepancy at the end of the movement. This transformation is close to a 33.7° counterclockwise rotation around the starting point. The final shift when the arm is on the target would be produced by a 18.3 diopter wedge prism. In the following, we will denote by *remapped target* the actual position of the finger when subject sees the visual feedback of the finger on the visual target (at the end of the exposure phase, the remapped target is 10 cm to the right of the visual target).

The post-test phase was identical to the pre-test except that the visuomotor discrepancy remained in place in the trials with visual feedback to prevent any decay of learning.

EXPERIMENT 2. The procedure was identical to *experiment 1* except for two differences. First, the training posture was *posture 3* instead of *posture 1*. Second, the final posture at the end of the movement was constrained. For this purpose, the blue cylinder aligned with the subject's forearm that was used to constrain the initial posture remained displayed during the movement. A green triangle was displayed (10-cm altitude and hypotenuse), one vertex on the target and its hypotenuse toward the viewer, to define a desired plane. Subjects were required to place the cylinder within this plane thereby constraining fully the degrees of freedom of the arm (except for wrist pronation). The orientation of the green triangle was chosen as the average plane of the arm in its "natural" final posture. This was computed from the average of four unconstrained pointing trials at the beginning of the experiment.

Data analysis

Trials where rigid body position was partly unavailable due to IREDs occlusion during movement or where the subjects occasionally did not point directly to the target were excluded from the analysis. The latter behavior occurred rarely and was usually due to subjects failing to realize that a pointing trial had started; in all cases initial direction differed from the desired horizontal movement by more than 30° in the sagittal plane. Faulty trials accounted for 0.86% of all trials.

Kinematics

Shoulder position was determined by calculating the point relative to the upper arm RB whose positional variance in Cartesian space was minimal. Elbow position was determined by calculating the point relative to the upper arm RB whose positional variance relative to the forearm RB was minimal (Biryukova et al. 2000). The four joint angles describing arm posture (upper arm azimuth, upper arm elevation, humeral rotation, elbow rotation) were defined as in Soechting et al. (1995). When necessary, the upper arm abduction angle (function of elevation and humeral rotation) was defined as the angle between the plane of the arm and the horizontal plane. Wrist pronation/supination was not studied.

Positional Optotrak data was numerically differentiated and filtered (Butterworth second-order filter, cutoff frequency: 5 Hz). The start of the movement was defined as the time when the hand speed first exceeded 3 cm/s. The average final finger location and covariance was calculated for each posture for both the pre- and post-test phases. Mean hand paths and 95% confidence areas were calculated by resampling at 100 evenly spaced points along the path length. Initial direction in Cartesian as well as joint space was measured by averaging instantaneous movement direction over the first 3 cm of movement. Hand azimuth was defined as the angle between the transverse x axis and the shoulder-hand axis.

RESULTS

Subjects found the task easy to perform and on informal questioning they were not aware of the visuomotor perturbation.

Adaptation as a function of initial posture

EXPERIMENT 1. During the pre-test phase subjects' pointing was very similar for the three different initial postures. This is shown in the distribution of trajectory endpoints in the frontal plane for the three postures (green-hued ellipses in Fig. 2A for two typical subjects; Fig. 2C for the group mean). Therefore pointing movements converge on the target whatever the initial posture of the arm. Subjects were then exposed to a visuomotor remapping and made pointing movements from only the most adducted posture (the "trained posture"). To assess the adaptation and its generalization, we examined the pointing movements as a function of initial posture in the post-test phase. These revealed substantial changes in subjects pointing behavior overall and as a function of the initial posture (red-hued ellipses in Fig. 2, A and C). First, pointing locations were all shifted compared to the pre-test phase in the direction appropriate for the visuomotor remapping (compare red- and green-hued ellipses). Second, the amount of adaptation decreased as

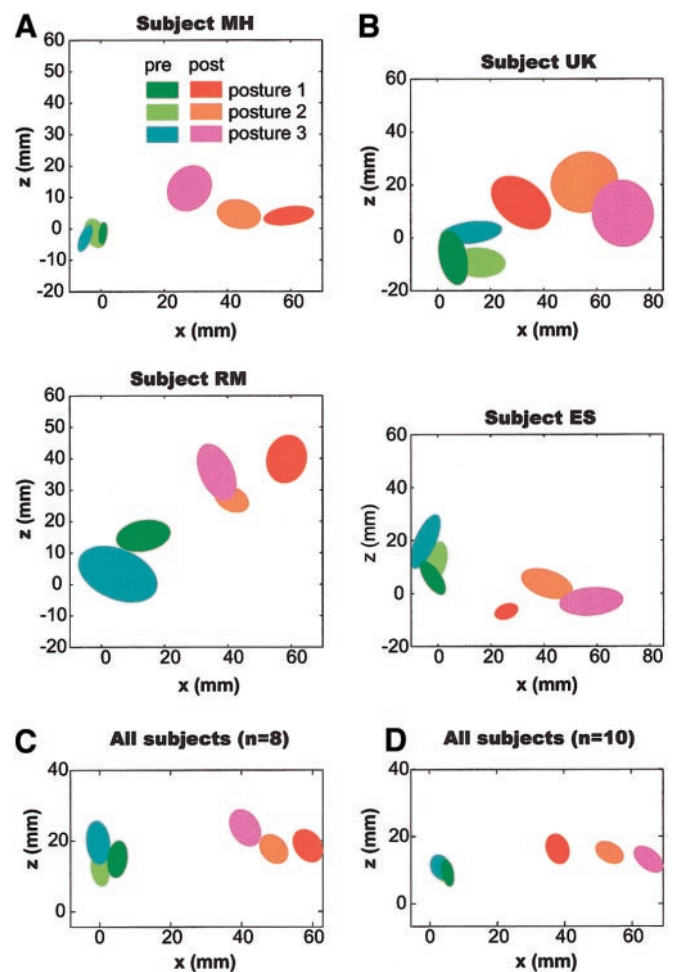


FIG. 2. A: *experiment 1*. Distribution of trajectory endpoints in the frontal plane for 2 representative subjects in the post-adaptation phase. Dispersion is estimated by the 95% confidence ellipses. In this figure, the origin of the axes corresponds to the position of the visual target. Colors identify the arm posture at the start of the movement. Cold colors: pre-test; warm colors: post-test. The trained posture was *posture 1* (red). B: *experiment 2*. Trajectory endpoints for 2 representative subjects. The trained posture was *posture 3* (purple). C and D: results for all subjects, in *experiments 1* and 2, respectively. A significant effect of the initial arm posture is found on the final finger position. This effect appeared along the perturbation axis only.

a function of the difference between the starting posture and the trained posture (compare the red ellipse for the trained posture with the more purple ellipses).

To quantify the amount of adaptation, we measured the change in the x pointing location as percentage of the displacement required to place the visually displayed finger on target (Fig. 3A). This confirmed that adaptation was not complete for any posture and adaptation decreases significantly as a function of the difference between the trained and the initial postures [$F(2,5) = 5.48, P < 0.01$]. The pointing errors with the left arm after adaptation of the right arm accounted for less than 10% of the maximum adaptation level (Fig. 3, \square). This demonstrates that little or no adaptation is due to a recalibration of vision (visual shift).

Figure 3C shows that adaptation level was nearly constant during the course of the post-exposure phase for all starting postures. Thus we can be confident that the global measures of adaptation calculated over the post-exposure phase correspond to a stationary adapted state.

To understand how adaptation is linked to arm posture, we analyzed the trajectory in intrinsic arm space. Figure 4 shows the distribution of final endpoints as well as the mean trajectory

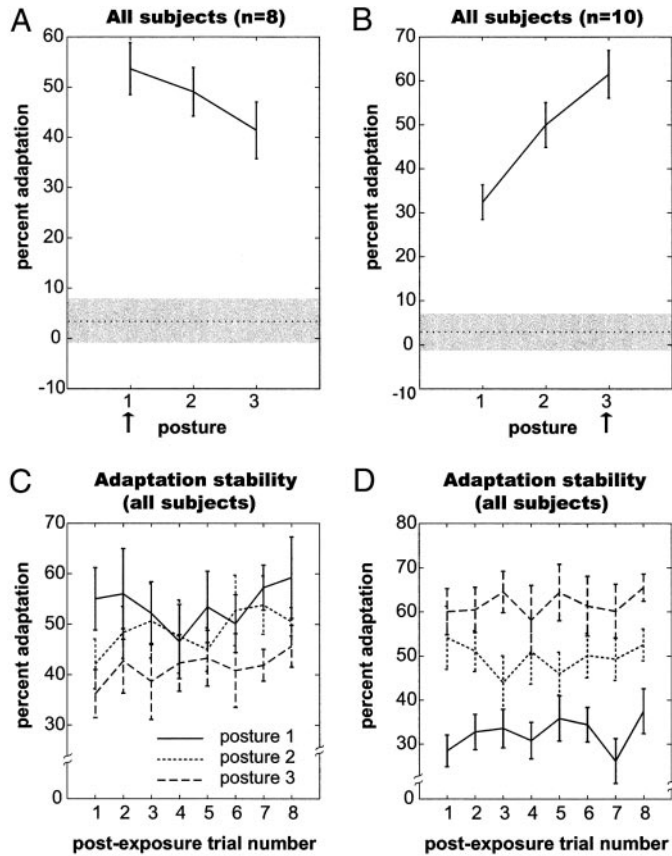


FIG. 3. Extent of the adaptation to the visuomotor discrepancy along the transverse x axis. **A:** *experiment 1*. Mean post-test adaptation as a function of arm initial posture. The trained posture is indicated (\uparrow). —, pointing with the right hand. . . ., pointing with the left hand. There was no constraint on initial left arm posture. Error bars and \square , 95% confidence intervals. **B:** same as in **A** for *experiment 2*. A converse pattern is seen, demonstrating that the generalization effect is relative to the trained posture. **C:** *experiment 1*. Adaptation level during the post-test phase, for all initial postures, as a function of trial number. Error bars: SEs. **D:** same as in **C** for *experiment 2*. The adaptation level did not change significantly during the course of the post-test phase.

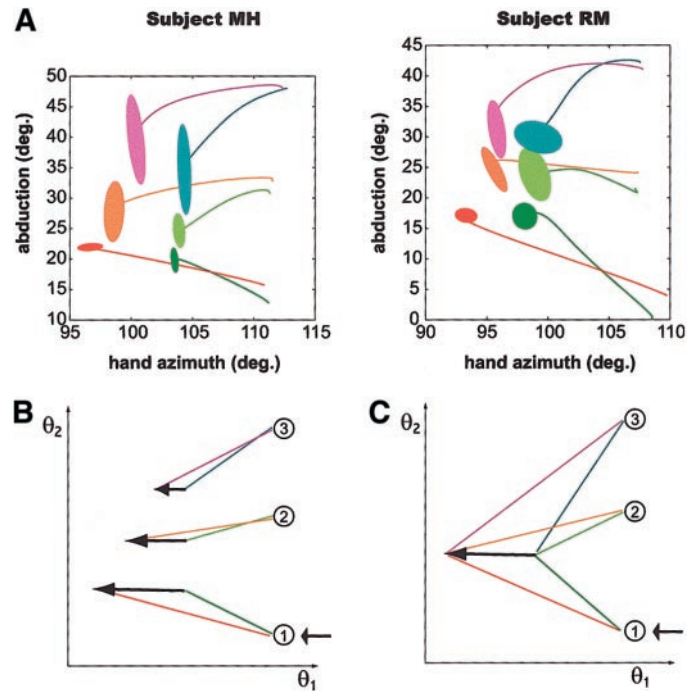


FIG. 4. **A:** *experiment 1*. Distribution of final postures in a 2-dimensional (2D) arm angle space for 2 subjects, as a function of the initial posture. Ellipses: 95% confidence zone of the endpoints. Solid lines: mean trajectory. Graphical conventions of Fig. 2. The final abduction angle is largely variable and depends on the initial abduction. **B:** schematic 2D drawing of the possible remapping of final proprioception in *experiment 1*. Solid lines: trajectories in joint space. Colors as in Fig. 2. Bold arrows, extent of the static proprioceptive remapping. Small arrow on the *right*, trained posture. In this hypothesis, the observed adaptation gradient in cartesian space is due to a local learning in final desired posture space. **C:** predictions in the case of a remapping of final proprioception when final posture is constrained to be identical before exposure. A complete transfer across initial postures is expected.

in the two-dimensional space of hand azimuth and arm abduction. These coordinates were chosen because the two angles are independent of each other when the hand is displaced along the axis of the visuomotor perturbation (x axis). The distribution of endpoints in the pre-test phase (green-hued ellipses) shows that variability is high along the abduction-adduction dimension. Moreover, final posture depends markedly on initial arm configuration. The same dependence of final posture on initial posture can be seen in post-test phase (red-hued ellipses); moreover, there is now a clear correlation between hand azimuth and abduction. Thus the differential adaptation observed in cartesian coordinates could be due to a simple positional remapping between visual target location and final posture. Alternatively, the adaptation could involve sensory or motor variables *during the execution* of the movement. The next section will clarify which of the two hypotheses holds.

Effect of constraining the final posture

The preceding results show that the adaptation generalizes only partially in Cartesian space, decreasing with the discrepancy between the initial and the trained posture. Two questions however remain to be answered. First, is the adaptation gradient specific to the trained posture or simply to *posture 1*? To check for this possible confound, *experiment 2* was performed training *posture 3*. Second, can adaptation be described as a

sum of a visual shift (here extremely limited) and a proprioceptive shift? It could indeed be argued that the generalization pattern is consistent with a remapping of the final arm proprioception. According to this hypothesis, the proprioceptive signals corresponding to the shifted arm position are associated with the neuronal code of “visual straight ahead”, updating thus the representation of arm posture. As the final posture depends on the starting orientation of the arm (Fig. 4A), this proprioceptive remapping would be only partial for the two untrained starting postures. To illustrate this, Fig. 4B is a cartoon of the results we obtained in *experiment 1*. The remapping due to the task is shown by solid arrows. The gradient of adaptation in Cartesian space can be explained by a gradient of visuo-proprioceptive remapping in joint space. However, if the final postures before exposure are constrained to be identical whatever the initial posture, the remapping would now lead to an equalization of the adaptation for all starting postures (single arrow on Fig. 4C). *Experiment 2* was also designed to test this prediction.

EXPERIMENT 2. In this experiment, we used the most abducted posture (*posture 3*) during the exposure phase and in addition constrained the final posture to be the same independently of the initial posture. Subjects were able to perform this task, and as shown in Fig. 5, pre-test final abduction was similar whatever the starting posture: differences were less than 4° for 9/10 subjects.

The results of Fig. 2 show a similar pattern of generalization whether or not final posture was constrained to be identical before exposure. In all respects, the results we found were very similar to the first experiment (Figs. 2B and 3, B and D). Again, the pattern of generalization in pointing showed aftereffects that were greatest for the trained posture and significantly decreased as the initial posture changed [$F(2,7) = 35.4$, $P < 0.001$]. Thus although final posture was similar before exposure, the posttest postures were significantly different depending on the initial posture (Fig. 5). These results answer the two questions that motivated this second experiment. First, as we used a different trained posture in this experiment, they demonstrate that the gradient is in relative terms and not absolute.

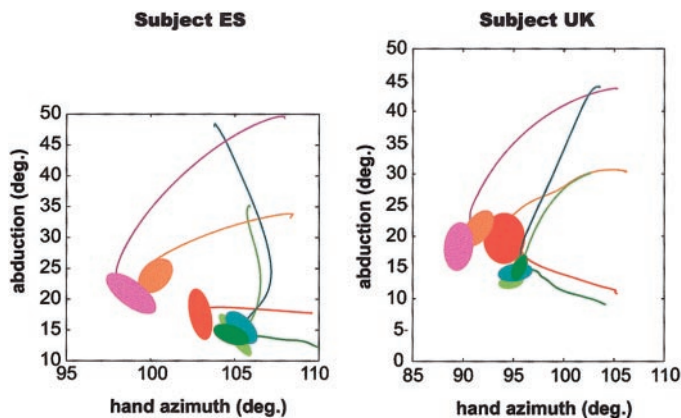


FIG. 5. *Experiment 2*. Final postures in 2D arm angle space for 2 representative subjects. Ellipses, 95% confidence zone of the endpoints. Lines, mean trajectory. Graphical conventions of Fig. 2. The final abduction is now constrained and shows no significant dependence on the initial abduction, showing that the subjects correctly reach the desired final forearm orientation. The lateral adaptation to the visual perturbation is, however, similar to *experiment 1* as can be deduced from the final hand azimuth.

Second, as the final posture was constrained, the adaptation gradient cannot be solely accounted by a remapping from terminal proprioception to terminal vision. Because the transfer of adaptation to the least adapted posture is approximately half of the maximum adaptation level (Fig. 3), we conclude that at least half of the adaptation depends on the particular arm movement that drives the finger onto the target.

It is interesting to note that the adaptation gradient was steeper in *experiment 2* than in *experiment 1*. This increased differentiation of the adaptation could be related to the decrease in pointing variability imposed by the additional constraint on final posture.

Feedforward and feedback control

Because a static shift in the relation between the visual goal and the position of the arm is not sufficient to explain the adaptation, we need to understand how the motor command is changed by the exposure to the new visuomotor mapping.

MOVEMENT DURATION. Movement velocity has been shown to condition visuomotor adaptation (Kitazawa et al. 1997). In consequence, we checked whether movements in the post-test phase had similar durations. Movement duration was not significantly different for initial *postures 1* and *3* in *experiment 1* [$F(1,7) = 0.81$, $P = 0.40$] as well as in *experiment 2* [$F(1,9) = 2.25$, $P = 0.17$]. We can thus rule out the possibility that the differential adaptation could be due to movement velocity.

INITIAL DIRECTION. To examine the components of adaptation, which is already present in the feedforward command, we analyzed the initial part of the trajectory before feedback could be processed. The initial direction of finger movement was calculated from the first 3 cm of the trajectory [between 60 and 260 ms into the movement depending on the subject, average 113 ± 28 (SD) ms for *experiment 1*, 113 ± 54 ms for *experiment 2*]. Figure 6 shows the initial direction measure in degrees in the horizontal plane from straight ahead for both the pre- and post-test phases. This shows that the change in the pointing response is already present at the beginning of the movement before sensory feedback is available. There were no significant differences in the initial direction in the sagittal plane (not shown). In the post-test phase, movements with visual feedback were interspersed between movements without visual feedback, to maintain a stationary adaptation level. In *experiment 1*, the initial direction of the reaching movements starting from *posture 1* differ significantly [$F(1,7) = 22.8$, $P < 0.002$] for trials with (■) and without visual feedback (□), suggesting that subjects initially corrected more when visual feedback was (predictably) not available. A similar difference was not observed in *experiment 2* for the movements initiated with *posture 3* [$F(1,9) = 1.99$, $P = 0.19$].

A differential adaptation in initial movement direction was not obtained in both experiments. The pre/post-exposure difference in initial direction varied significantly [$F(2,5) = 11.94$, $P < 0.001$] with initial posture in *experiment 1* but did not in *experiment 2* [$F(2,7) = 2.24$, $P = 0.14$]. Thus if the degree of deviation in the initial pointing direction is closely correlated with the final adaptation levels presented in Fig. 3 for *experiment 1*, this is not true for *experiment 2*. In contrast, the analysis in joint space reveals a differential adaptation in both experiments. We computed the pre/post-exposure change in

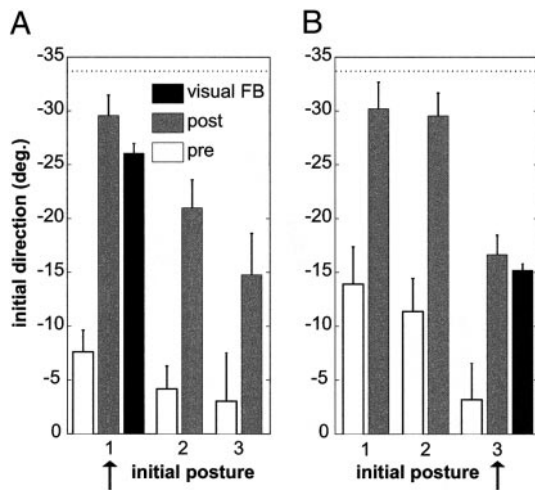


FIG. 6. Initial direction of pointing movements from straight ahead in the horizontal plane. □, pre-test; ▒, post-test; ■, trials with visual feedback during the post-test phase. Error bars: 95% confidence intervals. . . . direction of an ideal straight movement to the visual target. The trained posture is shown by an arrow. *A: experiment 1. B: experiment 2.* Significant differences in reaching are already present before sensory feedback is available.

initial direction in the four-dimensional joint space. In both experiments, this change depended significantly on the starting posture [MANOVA, Rao's $R(8,22) = 6.18, P < 0.001$ for *experiment 1* and $R(8,30) = 5.67, P < 0.001$ for *experiment 2*].

FINAL TRAJECTORY CORRECTIONS. The contribution of feedback processes to the movement should be most visible in the last part of the trajectory. To evaluate the importance of the on-line motor corrections in this task, we compared the mean trajectories for movements with and without vision made during the post-test phase (Fig. 7). In *experiment 1*, movements made with vision from the trained posture were curved outward (gray) while those without vision from this posture curved in the opposite direction (red, Fig. 7A). This shows that the ongoing movement is corrected towards the remapped target when visual feedback is available and corrected towards the apparent target position when visual feedback is absent. Movements made without feedback from the least adapted posture (purple, Fig. 7A) show little online correction.

The same pattern is seen for *experiment 2* (Fig. 7B, colors reversed because *postures 1* and *3* play reversed roles) suggesting that the difference in path curvature is not due to the initial posture per se.

DISCUSSION

In the present study, we investigated whether differences in initial posture could affect the adaptation to a visuomotor shift. We constrained the starting and final finger position to be the same for all conditions, but varied the initial posture, that is, the elbow abduction angle. Exposure to the visuomotor transformation was limited to movements initiated from a fixed initial posture, and graded generalization to other starting postures was observed. The reaching errors after exposure revealed a decrease of adaptation with increasing dissimilarity between the initial and trained postures. This was observed whether the "trained posture" was the most or the least abducted. This shows that adaptation is posture-specific and rules out the possibility that the gradient arises from different learn-

ing rates for different postures. Similar patterns of adaptation were seen whether the final posture was free (*experiment 1*) or constrained (*experiment 2*). This indicates that the pattern of generalization is unlikely to be due to a remapping between target position in visual space and a desired final posture.

A number of studies have examined the generalization of visuomotor adaptations. Baily (1972) and Kitazawa et al. (1997) studied the dependence of prism adaptation on the velocity of the movement. The first author reported little transfer from fast ballistic pointing movements to slow zeroing-in ones but a substantial transfer between slow movements and fast movements, in contrast with the velocity-dependent adaptation demonstrated by Kitazawa et al. (1997). The discrepancy between the two studies could be due to cognitive strategies that were excluded in the latter but not in the former study. In accordance with Kitazawa et al. (1997), we found that adaptation depended on the arm kinematics. This is partially inconsistent with the results of Freedman et al. (1965), who reported that adaptation during sagittal movements transferred to transverse movements. However, their task placed emphasis on pointing straight ahead as there was no visual target. In accordance to our data, prism adaptation acquired during the throwing of balls has been shown to be specific of the type of throw (overhand or underhand) (Martin et al. 1996) or of the inertia of the arm (Fernandez-Ruiz et al. 2000). Ghahramani and Wolpert (1997) showed that adaptation to a distortion of the visuomotor map could be differentially achieved depending on the starting location. However, initial posture as well as movement direction changed with the starting point. The present study demonstrates that variations in initial posture are sufficient to account for the differences in adaptation.

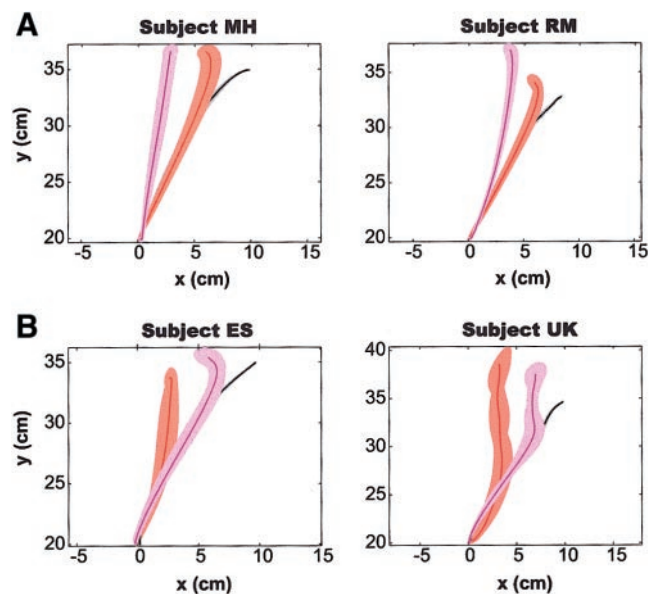


FIG. 7. Trajectories with and without visual feedback during the post-test phase. Lines are the mean trajectories in the horizontal plane, shaded zones are 95% confidence areas. *A: experiment 1.* Mean trajectories for 2 subjects. Gray, movement with visual feedback; red, movement without visual feedback, initial posture 1 (trained posture); purple, movement without visual feedback, initial posture 3. *B: experiment 2.* Mean trajectories for 2 subjects. Same initial posture-related color code as in *A*. The trained posture is now posture 3 (purple). When movements were initiated with the trained posture, the large initial adaptive deviation in movement direction was compensated in the middle of the movement by a distinct hook toward the visual target. This was not observed for movements initiated from the least adapted posture.

The observed impact of initial posture on adaptation to visuomotor rotations is at odds with the generalization in extrinsic space reported by Krakauer et al. (2000) after adaptation to a visuomotor rotation. Three facts can explain the discrepancy between that study and our observations. First, the visual feedback was shown here in three dimensions at or next to the actual finger position, whereas Krakauer et al. used a cursor on a monitor placed at 90° from the movement plane. Second, we gradually introduced the perturbation without subjects' awareness, whereas in the cited study, the rotation was full from the start and obvious to the subject. Last, the rotation was approximately half the angle used in their protocol. In fact, when large rotations are used, subjects show intermanual transfer (Imamizu and Shimojo 1995; in this study subjects were, however, trained in more than one movement direction). Overall, these differences suggest that the generalization in extrinsic space that was reported by Krakauer et al. could be due to the use of cognitive strategies that were excluded here.

Components of the visuomotor adaptation

Different levels of the sensorimotor transformation can have been affected by our adaptation procedure. A change in the processing of the visual information on finger and target position could occur. Similarly, proprioceptive information about arm posture or movement could be recalibrated by vision. Last, the generation of the motor commands (visual-to-motor translation) could be modified. These three different hypotheses will now be evaluated.

In both experiments, intermanual transfer was near to zero. This would not be observed if most of the adaptation was visual. This would indeed require the non-visual components of the adaptation in the (non-exposed) left arm to cancel out the visual adaptation. Moreover, the likely absence of visual recalibration can be related to several factors, known to also minimize the visual shift in prism adaptation: the subject's head was fixed as he looked through the 3D goggles (Wallace 1978); start and end points of the movement remained at the same location in visual space, in front of the subject so that gaze was never deviated to one side (no eye muscle potentiation was induced) (Paap and Ebenholtz 1976); visual feedback was available along all the trajectory (i.e. concurrent exposure, Cohen 1966; Cohen 1973); visual feedback of the hand at the beginning of the movement was veridical; and the visual world except the hand (especially the borders of the virtual space) was not displaced. Last, it is important to remark that the visual perturbation was a rotation around the starting point and not the eyes, hence remapping of the visual input would be complex and depend non-linearly on gaze position: for instance, the visual feedback of the hand at the beginning of the movement was always veridical, whatever the gaze position.

The other sensory input that could be recalibrated here is proprioception. Prism adaptation has been shown to induce a proprioceptive shift due to a re-establishment of the relationships between proprioceptive and visual signals (Harris 1965). Such a proprioceptive adaptation would logically depend on the complex relationships between arm posture and muscle spindle stretch during the movement. Thus this proprioceptive

remapping is difficult to characterize and its generalization is difficult to forecast. However, three facts argue for a limited proprioceptive adaptation in our experiments: first and foremost, a similar decrease of adaptation was observed whether final posture was constrained or not (*experiments 1* and *2*); initial finger kinematics and arm dynamics differed between pre- and post-test phases, though there was no visual-proprioceptive discrepancy at the starting location; and post-test finger trajectories were curved toward the visual location of the target for movements initiated from the trained posture, suggesting a proprioceptively driven corrective command. It is interesting to note that similar incomplete trajectory corrections have been observed when the arm is perturbed by inertial forces (Krakauer et al. 1999; Lackner and Dizio 1994), although no proprioceptive recalibration was involved in these experiments. The corrective hooks were absent for the least adapted posture. This could be due either to a small proprioceptive adaptation or to an under-threshold error signal. Taken together, these results suggest that, at most, only part of the aftereffects is attributable to a proprioceptive recalibration, and the shift it would entail is likely lower than the amount of adaptation measured for the least adapted posture.

If sensory adaptation is low or absent, the major part of the aftereffects must then be attributed to a change in the motor commands issued, that is, a modification of the visuomotor translation. This modification may be due to a conscious strategy (deliberate corrective response) or to a true visuomotor learning. The first hypothesis seems excluded here, as the visuomotor discrepancy was introduced progressively; debriefing at the end of the experiment confirmed that subjects were unaware of the perturbation. It is thus likely that observed changes were due to a genuine visuomotor adaptation process. The following section addresses its nature.

Visuomotor learning

Several mechanisms of visuomotor remapping can be proposed. Changes could affect either the planning or the execution of the movement, or both. The existence of a generalization gradient proves that what is learned is not simply a new endpoint trajectory, but pertains to the movement of the whole arm. The equilibrium-point theory (Feldman 1966; Hogan 1984) postulates that the final posture of the arm is predetermined when the movement starts (hypothesis of equifinality) (Kelso and Holt 1980). This would predict identical final postures in *experiment 2*, where the desired final posture is constant across conditions. As already noted, the converse is found.

Excluding the equilibrium-point theory, predefinition of the whole arm trajectory is still tenable if it involves displacements *relative to the initial posture* rather than absolute positions. It would be consistent with an initial posture-dependent adaptation. This view is, however, difficult to reconcile with the data as curvature of the finger trajectory is an evidence of the use of proprioceptive feedback in online movement corrections. In this respect, our results recall a similar curving of hand paths when the initial command is planned on the basis of a wrong estimation of hand position (Goodbody and Wolpert 1998). In our study, the alteration of the initial motor plan by the exposure to the visuomotor shift (demonstrated by the changes in

the initial portion of the trajectory) leads to the same type of corrections towards the visible target. This suggests that the final finger position cannot be accounted for by a mere remapping of the whole trajectory.

Can we still understand the generalization of initial movement changes? It is conceivable that this change in initial plan is identical for all initial postures, and the generalization gradient is merely due to its translation into a Cartesian endpoint trajectory. This hypothesis remains difficult to assess. The differences in adaptation could be due to a change in the planned kinematics or dynamics or to a modification of the muscle synergies at the beginning of the reach. A uniform change in initial finger direction is seen in *experiment 2*, but this was not found in *experiment 1*. It is unclear whether this difference between experiments is due to the change of trained posture or to the additional requirement of adopting a given final posture in *experiment 2*. Moreover, this uniform change was not found when analyzing data in joint space. This argues against a full generalization in initial kinematics. We have computed the inverse dynamics and examined the muscle torques at the beginning of the movement. Movement variability was however too high to unambiguously ascertain whether changes in initial active torques fully generalize across postures (as calculations done on average movement trajectories suggested). It is also possible that muscle synergies were globally modified (Thoroughman and Shadmehr 1999). However, electromyographic activity was not recorded in these experiments, and it is unclear whether significant differences could have been observed. Moreover, shoulder muscles contribute differently to shoulder torques as a function of posture (Buneo et al. 1997). Thus a global change in muscle activation could also lead to different amounts of adaptation. On the whole, a change in the muscle forces from the beginning of the movement would be consistent with the recent evidence of an interaction between kinematics and dynamics in visuomotor rotation tasks (Flanagan et al. 1999; Tong et al. 2002).

Arm posture is known to modulate the activity of cortical neurons in the parieto-frontal network: premotor and motor cortex (Bauswein and Fromm 1992; Caminiti et al. 1991), primary somatosensory cortex (Tillery et al. 1996), parietal areas 5 (Lacquaniti et al. 1995), 7m (Ferraina et al. 1997), and parieto-occipital area V6A (Battaglia-Mayer et al. 2000). In a protocol close to this one, Scott and colleagues demonstrated that neuronal activities in the motor cortex, dorsal premotor cortex, and area 5 depend on the arm posture, for identical hand position (Scott and Kalaska 1997; Scott et al. 1997). These modulations were observed during all behavioral epochs of the task (preparation, execution, target holding time). A subpopulation of neurons behaving similarly with wrist posture was found in the motor cortex by (Kakei et al. 1999). Thus the properties of the neural populations enable the central nervous system to differentially plan and execute pointing movements that share similar finger trajectories but involve different muscle synergies.

In conclusion, we have shown in this study that visuomotor adaptation is specific of the arm trajectory in joint space used during exposure. Moreover, in the present experimental conditions, adaptation involves a change in the translation from visual information to motor command. It remains now to be determined whether this change intervenes at the kinematic or at the dynamical level.

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