

Intra- and intermanual transfer of adaptation to unnoticed virtual displacement under terminal and continuous visual feedback

Alexandra Lenhard, Joachim Hoffmann, and Albrecht Sebald
Julius-Maximilians University of Würzburg, Germany

Participants trained aiming movements of the right hand to several targets with a prism-like virtual displacement of the location of one of the targets, receiving either terminal or continuous visual feedback. After training, the same targets were to be reached with the untrained left hand under manipulated feedback conditions. The right hand movements continuously adapted to the unnoticed visual displacement, significantly less with continuous than with terminal feedback. Under terminal but not under continuous feedback the adaptation to the manipulated target generalized to targets in the same horizontal direction but not to targets in the opposite direction. Finally, the movements of the untrained left hand showed the same qualitative changes to the targets as the movements of the trained right hand. The data are in line with the notion that the adaptation of the right hand movements is mainly based on a re-interpretation of target locations on which movement control of both hands draws.

It has long been noticed that training of a novel motor task with one limb can also improve performance of the untrained contralateral limb (e.g. Fechner, 1857; Bray, 1928). Since then, investigators have used a diversity of tasks to demonstrate intermanual learning transfer, for example, pointing under transformed visual feedback (Choe & Welch, 1974; Elliott & Roy, 1981; Imamizu, Uno, & Kawato, 1998), pursuit tracking (Hicks, Gualtieri, & Schroeder, 1983), maze learning (Stoddard & Vaid, 1996), mirror writing (Latash, 1999), or launching a cursor to a specified target position (Teixeira, 2000). However, despite the tremendous experimental effort, the mechanisms and structures underlying intermanual learning transfer are not yet fully understood.

Performing goal-directed movements generally poses a number of problems that have to be solved (cf. Saltzman, 1979; Imamizu & Shimojo, 1995; Imamizu, Uno, & Kawato, 1995; Rosenbaum, Loukopoulos, Engelbrecht, Meulenbroek, & Vaughan, 1996; Imamizu et al., 1998; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Vaughan, Rosenbaum, Harp, Loukopoulos, & Engelbrecht, 1998; Willingham, 1999). The actor has to select a spatial target for a movement that will achieve the environmental goal. To determine the target location, he or she uses retinal and extra-retinal visual information, as target position on the retina, accommodation, retinal disparity, vergence and others. However, reaching for the target also requires the determination of an adequate final posture, for example, a certain end position of the used

hand. Therefore, the target location has to be transformed from vision-based to effector-based coordinates. Furthermore, the trajectory from the current hand position to the target has to be determined and finally to be translated into an appropriate pattern of muscle activation.

However, it is yet unclear to what degree each of these processes contributes to intermanual learning transfer. Some researchers have suggested, that it is the learned pattern of motor commands which is transferred to the unpracticed hand (e.g. Hellebrandt, Parrish, & Houtz, 1947; Thut et al., 1996). If this holds true, then movements that are mirror-reversed versions of the practiced ones should profit the most from previous training of the contralateral hand. For example, a learned pattern of motor commands that causes the right arm to move from left to right would prompt a movement in the opposite direction if applied to homologous muscles of the left arm.

In line with this assumption, Thut et al. (1996) found that right-handers were more accurate in drawing meaningless figures with the right arm if they had previously practiced the drawing of mirror-reversed versions of the same figures with the left arm. However, this study did not provide a comparison between transfer that results from previous training of mirror-reversed to previous training of non-reversed figures. Furthermore, the practice figures consisted of basic elements (lines and semi-circles), each of which could also be found in its mirror-reversed version in at least one other practice figure. Therefore it cannot be excluded that participants would have profited equally from previous contralateral training of non-reversed figures.

Hicks, Gualtieri and Schroeder (1983) compared the extent of intermanual learning transfer of reversed as opposed to same-direction movement patterns. They used a pursuit tracking task with either clockwise or counter-clockwise movements. Mean time on target in the transfer phase was longer for reversed than for same-direction movements. However, this was only true for extended original training.

Other researchers have claimed that intermanual learning transfer occurs because the actor learns a new

Alexandra Lenhard, Joachim Hoffmann, and Albrecht Sebald, Psychologisches Institut III, Julius-Maximilians University of Würzburg, Germany.

We thank Georg Schüssler for his help in constructing the apparatus; and André Klassen and Christian Stöcker for checking and improving the English.

Correspondence concerning this article should be addressed to Alexandra Lenhard, Psychologisches Institut III, Julius-Maximilians University of Würzburg, Röntgenring 11, 97070 Würzburg, Germany. Electronic mail may be sent to lenhard@psychologie.uni-wuerzburg.de.

mapping of vision-based target coordinates onto effector-based target coordinates which can be generalized to the contralateral limb (Latash, 1999; Imamizu et al., 1998). As virtually any part of the body can serve as an effector, it would appear that the brain must provide multiple effector-based spatial representations. In fact, recent neurological and behavioral data indicate that signals from a variety of modalities (e.g. vision, proprioception, audition, vestibular sensation) are combined to form a distributed representation of space in the posterior parietal cortex (Brotchie, Andersen, Snyder, & Goodman, 1995; Andersen, Snyder, Bradley, & Xing, 1997). This representation can be used to construct multiple frames of reference, for example object-centered, eye-centered (Colby, 1998), head-centered, trunk-centered (Andersen et al., 1997), and arm-centered (McIntyre, Stratta, & Lacquaniti, 1998) frames of reference. Kalaska, Scott, Cisek, and Sergio (1997) proposed that the distributed representation of space may be the core of a powerful mechanism that provides coordinate transformations into multiple effector systems. If this holds true then changes in this distributed representation of space should affect different effector systems. These changes may therefore constitute the basis of interlimb learning transfer.

In accordance with this proposition, Imamizu et al. (1998) demonstrated, that participants who had learned an artificial transformation of elbow- and shoulder-joint angles during an aiming task, tended to apply the same transformation when aiming with the unpracticed hand. The researchers assumed that the participants had acquired a new internal model of kinematics represented in terms of joint angles in a shoulder-centered frame of reference. According to their model, the adjustments had been made to a central representation not specific to either arm but common to both arms. However, two questions must be considered. First, both transfer of motor commands and acquisition of a new internal model of kinematics that is represented in joint angles could account for the presented data, because both models equally predict benefits for mirror-reversed movements of the unpracticed hand. (Note that the same configuration of joint angles for both arms corresponds to mirror-reversed arm postures.) In fact, the results of the study indicate that the mean aiming bias of the unpracticed hand was lower under mirror-reversed conditions than under non-reversed conditions. Second, the participants were informed about the transformation of joint angles prior to the learning phase. Therefore, the generalized adaptation could have been due to strategic processes rather than due to a new internal transformation of joint angles (cf. Willingham, 1999).

Another way to modify the link between sensory input and motor output consists in the use of prism wedges (e.g. Choe & Welch, 1974; Elliott & Roy, 1981). However, there is an important difference between prismatic displacement and the manipulation that was used by Imamizu et al. (1998). A prismatic displacement can be expressed as a linear transformation in object-centered (extrinsic) coordinates but becomes nonlinear and complex when represented in joint-angles. Imamizu et al. used a transformation that was linear in joint angles but nonlinear in object-centered coordinates. They proposed that the CNS would preferably adjust to linear transformations. If this is the case, then adaptation to prismatic displacement should rather affect an object-centered representation of space, than a representation of space in joint angles of the arm (see also Rogosky & Rosenbaum,

2000, for a discussion of space-based vs. joint-based distortions of visuomotor transformations). Furthermore, if this adaptation of coordinate transformation is not restricted to the practiced hand, then intermanual learning transfer of prismatic adaptation should engender parallel but not mirror-reversed versions of the originally performed movements. Consider, for example, a prismatic displacement that shifts the visually perceived target location 10° to the right. To counteract this displacement, the actor could—consciously or not—learn to mentally shift the target location 10° to the left. If this re-interpretation of the visually perceived target location generalizes to unexposed limbs, the actor would adjust the direction of left hand movements as well as right hand movements to the left side; however, different joint angles of the two arms would be required.

Accordingly, negative aftereffects have been shown both for exposed and unexposed limbs after adaptation to prismatic displacement (Helmholtz, 1866, as cited in Prinz, 1992, pp. 67-68; Choe & Welch, 1974; Elliott & Roy, 1981). However, the influence of explicit knowledge of the prismatic displacement on adaptation is still unclear. As Willingham (1999) stated, conscious motor control can replace perceptual-motor integration processes.

To provide further evidence that the effects of intermanual learning transfer were actually based on a new internal transformation of target coordinates, Latash (1999) used a mirror writing paradigm. Students practiced writing a sentence with the dominant hand while looking in a mirror that was positioned behind the paper. The sentence should appear correctly in the mirror, not on the paper. Both writing speed and errors during post-test indicated a high degree of learning transfer to the non-dominant hand. Note that the untrained hand had to trace the same trajectory as the trained one, that is, movements of the untrained hand were non-reversed—not mirror-reversed—versions of the practiced ones. Therefore, the results cannot be taken as evidence for a generalized re-mapping of joint angles. Rather they point to an effector-unspecific remapping of vision-based coordinates.

To summarize, profit from previous contralateral training has been demonstrated for mirror-reversed as well as for non-reversed versions of the originally practiced movements. Both transfer of motor commands and transfer of coordinate remappings may partially account for intermanual learning transfer. However, it is still unclear to what degree this is the case for each single process. Furthermore, a detailed examination of transfer of non-reversed movements could possibly clarify what kind of effector-unspecific spatial representations the CNS provides and how they affect movement planning.

Objectives and General Method

The goal of the present study was to further contribute to the issue whether intermanual learning transfer is based on a re-interpretation of the visually perceived target locations or on a transfer of muscle-specific motor commands. For this purpose, we used an experimental set-up introduced by Wolpert, Gharamani, and Jordan (1995) in which visual feedback of the hand could be displaced for an individual target. The participants were trained to perform a task that resembled dialing telephone numbers on a push-button telephone with their right

hand. They had no direct view of the hand during the task. Instead, a virtual spot represented the position of the hand. Flat numbered squares depicted the “push-buttons” (see Fig. 1). Each critical movement started from a square in the middle column and aimed at one of the neighboring squares to the left or to the right side. For one single target in the right or left column we manipulated the feedback. The virtual spot indicated that movements to this target were shorter than actually carried out. Accordingly, the visual feedback signaled a hit when the real position of the hand was beyond the target square. As we intended to prevent strategic movement adaptation, the virtual displacement of the critical target was set small enough to remain unnoticed. In order to determine the degree of learning transfer, performance of the left and the right hand was tested before and after the exposure phase. During the pre- and posttest phase, visual feedback was given which always indicated a hit for any aiming movement that ended outside of the starting square. Consequently, feedback dependent learning was prevented in these pre- and posttest phases.

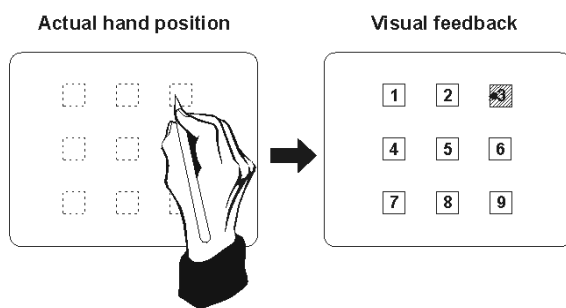


Figure 1. Display with feedback representing the hand position. Direct view of the hand was prevented. Instead, the virtual image of the display appeared in the plane of the hand. A blue spot represented the position of the hand in three-dimensional space. To provide the possibility of measuring the hand position, the participants performed the task holding a stylus in their hand.

According to the given evidence in the literature, we expected that the right hand would adapt to the virtual displacement so that the movements to the manipulated target would become continuously longer. Furthermore, we expected that this adaptation would transfer to movements of the untrained left hand in the post-test phase. With regard to the type of transfer, two different outcomes are to be considered:

If intermanual learning transfer is based on a re-interpretation of the visually perceived location of the manipulated target, movements of the untrained left hand to this target should be influenced in the same way as movements of the trained right hand. Thus, if the right hand has learned to make larger movements to the manipulated target, the left hand should also show larger movements to the manipulated target. If, however, the intermanual transfer is based on muscle-specific motor commands, the adaptation of the right hand should be transferred to movements of the untrained left hand which require contractions of homologous muscles, i.e. to mirror-reversed versions of the adapted movements. Thus, if the right hand has learned to make larger movements to the manipulated target, the left hand should show larger movements to the target vis-à-vis of the manipulated target as these movements address just the

muscles which are homologous to the muscles addressed by the right hand to reach the manipulated target.

As the visual-motor mapping was selectively manipulated for only one of the targets the present study also allows to examine whether or not adaptation to the manipulated target generalizes to other targets. This issue has been controversially discussed as well:

Bedford (1989) suggested that a mapping between visual and motor coordinates is neither to be characterized as a list of independent pairs, nor may the system be so constrained that only the simplest mappings are learned. Instead, she described the process of learning a new coordinate transformation as “looking for a relation between an entire dimension of stimuli and an entire dimension of responses, rather than associating each individual stimulus with each individual response”. According to Bedford, a linear fitting would be preferred even when more adaptive non-linear solutions exist. Consequently, in the present study movements to non-manipulated targets should be influenced more strongly the nearer they are located to the virtually displaced target.

By contrast, Ghahramani and Wolpert (1997) have proposed a computational model of modular learning known as the “mixture of experts”. This model holds that individual mappings are learned for each pair of starting and target location, constituting “experts”. Generalizations to new pairs are assumed to be accomplished by a weighted average of the learned pairwise visuomotor mappings. As in the present experiment all required pairs of starting and target locations are trained, every pair should constitute an “expert” on its own behalf. Consequently, the virtual displacement of one target should affect movements only to this but not to other targets.

Experiment 1

Method

Participants

Twenty-eight undergraduate students (24 females, 4 males) from the University of Würzburg, ranging in age from 19 to 37 years, participated in the study in fulfillment of a course requirement. All participants were right-handed, as determined by the Lateral Preference Inventory (Coren, 1993) and were naive as to the nature of the experiment. Each student was tested in a single session lasting approximately 40 min.

Apparatus and Stimuli

Participants sat in front of a digitizing tablet (Intuos Graphics Tablet A5) and held a stylus in their hand (Fig. 2). To provide a comfortable arm position, the forearm rested on a little pillow about 15 x 13 cm of size. A semi-silvered mirror that was suspended in a horizontal plane 23 cm above the tablet prevented direct view of the arm. The position of the stylus as defined by its point was measured on-line and determined successive x- and y-coordinates of the performed trajectories. The data were sampled at a rate of 20 Hz by a PC with AMD Athlon Processor (1.01 GHz). A Samsung Sync Master 90092 screen (1024 x 768 pixels) was fixed to a metal support so that its front was positioned in a horizontal plane 23 cm above the mirror. One pixel measured 0.35 mm on the screen. The display including feedback of hand position (see Fig. 1) was depicted in mirror-reversed version on this screen. Looking down at the mirror the participants viewed the reflected image of the display. Because the mirror was positioned exactly in the middle between the tablet and the screen, an upright virtual image of display and feedback appeared in the plane of the digitizing tablet. The

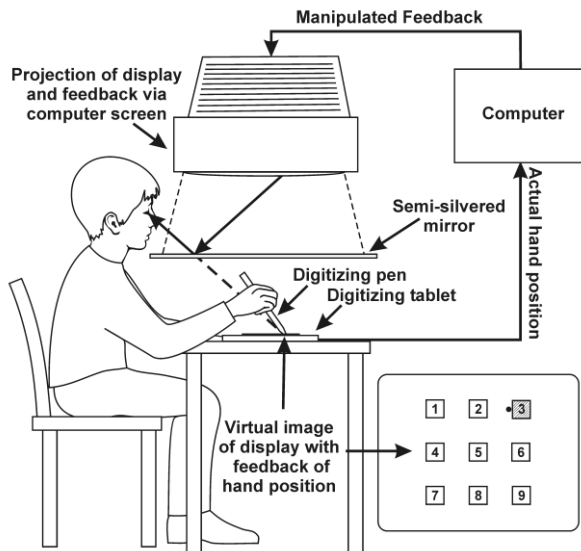


Figure 2. Experimental set-up for recording aiming movements under manipulated visual feedback. The position of the hand was measured on-line via digitizing tablet. A computer calculated the manipulated feedback. The display including a blue spot that represented the hand position was projected on a semi-silvered mirror. The reflection of the mirror produced a virtual image of the display in the plane of the hand.

display consisted of a large gray square (200 x 150 mm) with nine white numbered squares on it measuring 13 x 13 mm each. The distance between neighboring squares was 19 mm. A blue cursor spot of 4 mm in diameter represented the feedback of hand position, which was up-dated on-line according to the measured coordinates.

Procedure

Each participant was assigned randomly to one of six groups. The groups differed with respect to the target square for which manipulated feedback was given. (Note that for squares of the middle column correct feedback was always provided.)

To familiarize the participants with the equipment, we illuminated the semi-silvered mirror from below at the outset of each experimental session. Both the cursor spot and the hand were then visible. We demonstrated to the participants that the point of the stylus and the cursor spot corresponded for every single position of the hand.

The participants were informed that their task would be to hit the center of subsequently marked squares with the point of the stylus. The movements had to be performed like dialing a telephone number, not like drawing lines on a paper, that is, contact between stylus and tablet was allowed only at the beginning and the end of each movement. Within each critical trial, participants started on a square in the middle column (squares "2", "5", or "8") and aimed at one of the neighboring squares to the left or to the right side. For example, starting square "2" was followed by target squares "1" or "3" only. Consequently, six pairs of starting and target locations existed, each of which constituted one critical trial. The order of the critical trials was quasi-randomized. The first trial of each experimental block started on the central square (square "5") which was marked in green color. Immediately after touching the virtual position of the starting square on the tablet, its color changed to red, indicating a hit. After 100 ms, the square became white again and the subsequent target square lit up with green color. This procedure was continued to mark the sequence of starting and target squares. We instructed the participants to make the movements as quickly but as accurately as possible. In addition, the participants were asked to prevent contact between tablet and forearm. During the experiment the room was darkened except for the light from the upper screen. As a consequence, the hand was then invisible.

Pretest phase. The purpose of the pretest phase was to assess how accurately participants would hit the target squares without seeing their hands, before they had received any training. Two blocks with 36 trials each were performed. Half of the participants performed the first block with the right hand and the second block with the left hand. For the remainder the order was reversed. Because we wanted to prevent feedback dependent learning during the pretest but nevertheless had to guarantee adequate starting positions for each critical trial, feedback was given as follows: Hand positions were correctly fed back by the blue spot only if participants aimed at one of the squares in the middle column (i.e., squares "2", "5", or "8") and the stylus touched the tablet. By this it was ensured that in all critical trials movements really started from one of squares in the middle column. However, as soon as the stylus was lifted to move to the next target (i.e., squares "1" or "3", "4" or "6", "7" or "9"), the blue spot was suppressed and a hit was fed back as soon as the stylus touched the tablet outside of the starting square regardless whether the target was actually hit or not. By this false feedback, learning about the appropriate movements from the starting squares in the middle column to the targets on the left and right side was prevented. There was a time limit of 250 s for each block. However, none of the participants missed this criterion. Participants needed about 4 minutes to complete both blocks of the pretest.

Exposure phase. The purpose of the exposure phase was to train participants with a virtual displacement of a single target. For each of the six groups, visual feedback was manipulated for one particular target. The virtual spot indicated that aiming movements to this target were shorter than actually carried out. The relation between the real hand position on the tablet $P(x, y)$ and the position $V(x^*, y^*)$ that was presented via virtual display is described in the following equations:

$$\begin{aligned} x^* &= 0.62 \cdot (x - x_{\text{start}}) + x_{\text{start}} \\ y^* &= y, \end{aligned}$$

where x_{start} corresponds to the starting position of the relevant trial as measured on-line. As a consequence, the cursor spot indicated a hit in the center of the target square when the actual end position of the movement lay approximately 20 mm beyond (see Fig. 3). For all other target locations the relation between hand position and cursor spot remained unperturbed.

The exposure phase consisted of six blocks with 72 trials each. Throughout this phase the cursor spot was visible each time the stylus touched the tablet. This kind of feedback is generally referred to as terminal (cf. Cohen, 1967; Uhlarik &

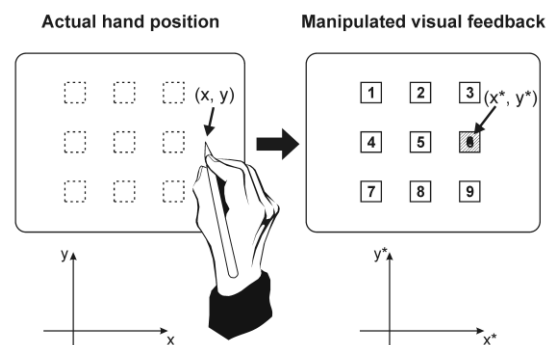


Figure 3. Manipulation of visual feedback. The virtual spot indicated that movements to one particular target were shorter than actually carried out (the figure depicts manipulation for target "6"). As a consequence, the cursor spot indicated that the target square had been hit in the center when the actual end position of the movement lay 20 mm beyond. (x, y) denote the Cartesian coordinates of the hand position on the tablet, (x^*, y^*) denote the manipulated hand position that was fed back via virtual display.

Canon, 1971; Imamizu & Shimojo, 1995). All participants used their right hand. At the end of each block, an on-screen message encouraged the participants to further improve their performance and instructed them to start the next block whenever they felt ready to do so. Participants needed about 20 minutes to complete the six blocks of the exposure phase.

Posttest phase. A posttest which was identical to the pretest was performed immediately after the last exposure trial. The purpose of the post-test was to assess the influence of the virtual displacement on movement end positions in comparison to the pretest.

Postexperimental interview. After finishing the posttest, participants were asked whether they had noticed anything peculiar about the experiment. Four participants answered that they had become aware of the virtual displacement and correctly indicated the manipulated target. These participants were excluded from further analysis. All other participants seemingly did not notice the target specific feedback manipulation.

Data Reduction and Analysis

For each trial, performance time (PT, starting with target onset) and end position (x_{end} , y_{end}) of the first aiming movement were extracted from the collected data, regardless of whether the target was really hit or not. From these raw data a transversal aiming bias was determined for each block and target. The aiming bias was calculated as the mean horizontal distance between the displayed center of the target square and the end position of the first aiming movement (x_{end}), so that positive values indicate overshoots and negative values indicate undershoots. Furthermore, the differences between the aiming bias of the posttest and the pretest for the right and the left hand, respectively, were calculated. Positive differences indicate that movements to a certain target became longer after exposure to the manipulation. Finally, the amount of intermanual learning transfer was assessed by comparing the pre-post-differences of the left and the right hand.

Four movement conditions were distinguished regarding the feedback manipulation: (a) movements to the manipulated target (MT), (b) movements to a target in the same column as the manipulated target (SC), (c) movements to the target vis-à-vis of the manipulated target (VV), and (d) movements to a target diagonally opposite the manipulated target (DO).

Statistical comparisons were typically carried out with analyses of variance (ANOVAs). As the prerequisite of sphericity was supposed to be violated because of the different movement conditions, we applied Greenhouse-Geisser-corrections in the case of repeated measures. Post-analysis was performed with one-way ANOVAs and Student's t-tests. We used the Bonferroni-Holm-procedure to adjust for multiple post-comparisons. If not otherwise stated, the criterion of significance was set at $p < .05$.

Results and Discussion

Learning Process

To assess the learning process, we analyzed transversal aiming bias and performance time during the exposure phase with separate 6×4 (Block \times Movement Condition) ANOVAs with repeated measures. Mean transversal aiming bias and performance time are plotted in Fig. 4 as a function of movement condition and block.

Transversal aiming bias. The feedback manipulation differentially affected the transversal aiming bias. Analysis yielded main effects of movement condition, $F(1.54, 35.44) = 57.99$, $p < .001$, and block, $F(3.44, 79.18) = 12.07$, $p < .001$, which were modified by a Block \times Movement Condition interaction, $F(7.73, 177.78) = 6.50$, $p < .001$. Post-ANOVAs for every single movement condition revealed main effects of block both for condition MT, $F(3.71, 85.31) = 18.35$, $p < .001$, and condition SC, $F(3.58, 82.40) = 12.88$, $p < .001$. There

was a weaker effect of block for condition VV, $F(3.56, 81.97) = 3.41$, $p < .05$, but no effect for condition DO. At the end of the exposure phase, condition MT showed the strongest aiming bias ($M = +6.08$ mm, $SE = 0.64$ mm), followed by SC ($M = +1.81$ mm, $SE = 0.51$ mm). Pairwise comparisons indicated that differences of aiming bias for block 8 existed between any two movement conditions ($p < .01$ for all tests) except between conditions VV ($M = -0.46$ mm, $SE = 0.54$ mm) and DO ($M = -1.20$ mm, $SE = 0.47$ mm).

These results indicate that participants adapted to the feedback manipulation with their right hand. At the end of the exposure phase, movements to the manipulated target were larger than movements to all other squares. Furthermore, learning was not restricted to the manipulated square but also affected movements to targets in the same direction. They were smaller than movements to the manipulated square but larger than movements in the opposite direction. An unexpected finding was the small but significant main effect of block for condition VV. At first sight, one might assume that the learning of larger movements also generalizes to the target vis-à-vis of the manipulated square. In our opinion, there is considerable tendency to undershoot all targets before the exposure

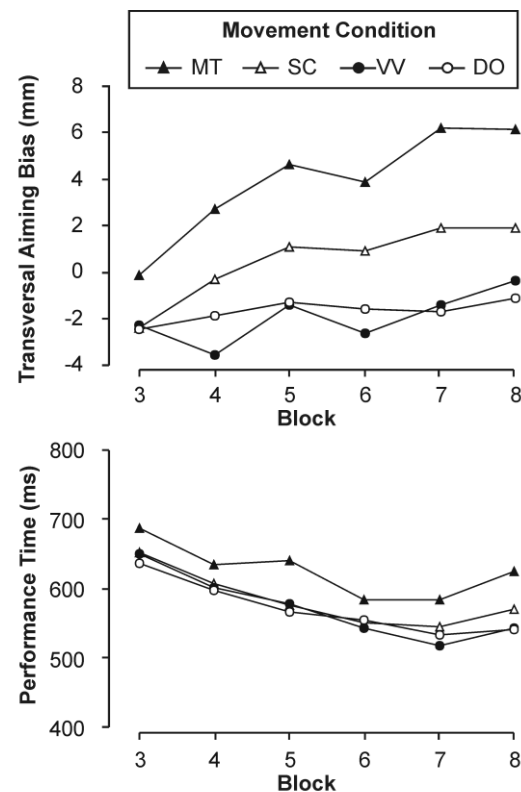


Figure 4. Mean transversal aiming bias (upper panel) and performance time (lower panel) as a function of movement condition and block during the exposure phase in Experiment 1. The movement conditions were: MT (movements to the manipulated target) vs. SC (movements to a target in the same column as the manipulated target) vs. VV (movements to the target vis-à-vis of the manipulated target) vs. DO (movements to a target diagonally opposite the manipulated target). The exposure phase comprised blocks 3 to 8. Aiming bias and performance time referred to the first touch between stylus and tablet outside of the starting square.

reason to doubt this assumption. First of all, participants phase. (This result is consistent with previous findings of Carlton, 1979.) A 2×4 ANOVA (Hand \times Movement Condition) for the aiming bias of the pretest phase showed that this effect was stronger for the right ($M = -5.39$ mm, $SE = 1.16$ mm) than for the left hand ($M = -2.28$ mm, $SE = 1.46$ mm), $F(1, 23) = 6.95$, $p < .05$. There were no initial differences between the movement conditions, nor was there a significant interaction of hand and movement condition. Thus, learning to reduce the aiming bias in general during the exposure phase might have affected the movement length in condition VV. However, at the end of the exposure phase, participants still undershot the targets in conditions VV and DO, whereas they overshot the targets in conditions MT and SC. Furthermore, there were no significant differences of aiming bias between conditions VV and DO at the end of the exposure phase. These results suggest that the small change of movement length in condition VV during the exposure phase was rather due to an unspecific reduction of aiming bias than an effect of the critical feedback manipulation.

Performance time. Analysis of performance times yielded a main effect of block, $F(2.96, 67.98) = 14.88$, $p < .001$, indicating an overall decrease of performance time. There was also a main effect of movement condition, $F(2.03, 46.59) = 7.30$, $p < .01$, but no significant Block \times Movement Condition interaction. Pairwise comparisons revealed that mean PT of condition MT ($M = 626.28$ ms, $SE = 26.33$ ms) was longer than that of any other condition was (SC: $M = 583.52$ ms, $SE = 23.91$ ms; VV: $M = 572.94$ ms, $SE = 21.70$ ms; DO: $M = 572.33$ ms, $SE = 22.41$ ms; $p < .05$ for all tests). The remaining comparisons failed to reach significance.

Two possible explanations might account for increased PTs in condition MT. On the one hand, larger movements generally need more time to be executed. Fitts' Law (Fitts, 1954) assumes a logarithmic relation between movement time and movement length. On the other hand, the induced discrepancy between vision and proprioception might require an additional effort for movement programming and therefore lead to longer response latencies. To decide between these two possibilities, we further examined PTs of every single block with one-way analyses of covariance that controlled for movement length. We found a significant main effect of movement condition for block 7, $F(3, 68) = 5.61$, $p < .01$, and nearly significant effects for blocks 3, 5, and 6 ($p < .1$ for all tests). Therefore, longer PTs in condition MT seem to be not only an effect of movement length but also an effect of additional programming effort induced by the feedback manipulation.

Learning transfer

We analyzed the differences between the transversal aiming bias of posttest and pretest phase with a 2×4 (Hand \times Movement Condition) ANOVA with repeated measures to assess the amount of intermanual learning transfer. Mean pre-post-differences of the transversal aiming bias are depicted in Fig. 5 as a function of movement condition and hand.

There was a clear effect of movement condition, $F(1.82, 41.79) = 14.72$, $p < .001$. Participants showed the highest pre-post difference under condition MT ($M = +9.75$ mm, $SE = 1.23$ mm), followed by SC ($M = +7.43$ mm, $SE = 1.08$ mm). Pairwise comparisons revealed that the difference between these two conditions approached

significance, $t(23) = 2.89$, $p = .05$, as did the difference between SC and VV, $t(23) = 2.86$, $p = .05$. Any other two movement conditions differed from each other, ($p < .05$, for all other tests), except conditions VV ($M = +3.70$ mm, $SE = 1.37$ mm) and DO ($M = +3.33$ mm, $SE = 1.39$ mm). Neither the main effect of hand nor the Hand \times Movement Condition interaction reached significance.

These results clearly indicate that intermanual learning transfer has taken place. For both hands, movements to the manipulated target were larger than movements to other squares after exposure to the feedback manipulation. Moreover, we found no significant differences between the right and the left hand. The transfer of learning in condition MT was as high as 83.0 %. For movements in condition SC the pre-post-difference was even slightly larger for the left than for the right hand. Obviously, both hands adapted to the manipulation in the same way. Therefore, a transfer of motor commands to homologous muscles of the left arm or hand can be ruled out as explanation for the observed learning transfer. It would rather appear that the same re-interpretation of target locations was used to control the aiming movements of both hands.

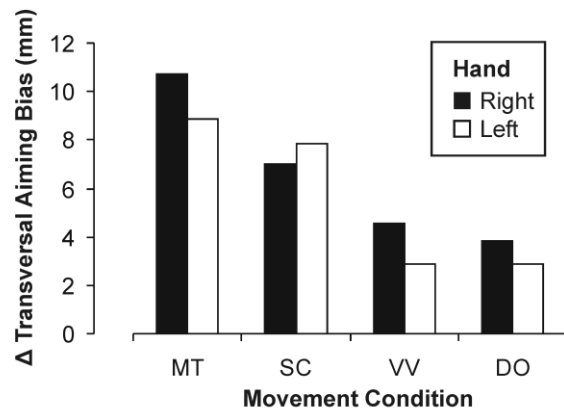


Figure 5. Mean pre-post-differences of transversal aiming bias as a function of hand (right vs. left) and movement condition (MT [movements to the manipulated target] vs. SC [movements to targets in the same column as the manipulated target] vs. VV [movements to the target vis-à-vis of the manipulated target] vs. DO [movements to targets diagonally opposite the manipulated target]) in Experiment 1. Note that only the right hand was trained with a target-specific visuomotor transformation during the exposure phase. Positive values of this difference indicate that movements to a certain target square were longer in the posttest than in the pretest phase.

Generalization to Other Targets

An additional objective of this study was to examine whether adaptation to the feedback manipulation would generalize to non-manipulated targets. Remember that the mixture of experts model (Gharamani & Wolpert, 1997) suggests a modular system based on separate visuomotor mappings for each learned pair of starting and target locations. Accordingly, no differences between the aiming bias of conditions SC, VV, and DO would be expected, as the respective visuomotor mappings remained unperturbed during the experiment. However, after the exposure phase, movements in condition SC were larger, than movements in conditions VV and DO. This finding speaks against the notion that under the present conditions the adaptation took place for each pair of starting- and target locations separately. Rather, there seems to be a tendency to find comprehensive "rules"

which cover an extended spectrum of movements. Bedford (1989) suggested that preferably “rules” are defined that represent linear interpolations. She termed that the *intermediate linear constraint*. To test her model, we considered only those participants who experienced manipulated feedback for a target on one corner of the display (i.e., targets “1”, “3”, “7”, and “9”). In these cases condition SC could be subdivided into (a) movements to the adjacent target and (b) movements to the distant target. For example, if target “1” was manipulated, movements to the adjacent target “4” and to the distant target “7” were analyzed separately.

We performed a 2×3 ANOVA (Hand \times Movement Condition) with repeated measures considering pre-post-differences only for movements to targets in the manipulated column. The three different movement conditions were: MT (movements to the manipulated target) vs. SC_{near} (movements to the adjacent target) vs. SC_{distant} (movements to the distant target). Mean pre-post-differences of the transversal aiming bias are depicted in Fig. 6 as a function of movement condition and hand.

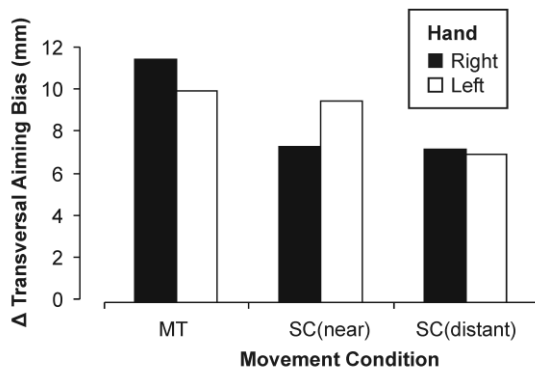


Figure 6. Mean pre-post-differences of transversal aiming bias for movements to the manipulated column in Experiment 1. The three different movement conditions were: MT (movements to the manipulated target) vs. SC_{near} (movements to the adjacent target in the same column) vs. SC_{distant} (movements to the distant target in the same column). Note that only those participants are included for which the manipulated square was seated on one edge of the display (i.e., targets “1”, “3”, “7”, and “9”, $N = 16$).

The pre-post-differences of transversal aiming bias were differentially affected by the three movement conditions, $F(1.91, 28.61) = 4.51, p < .05$. Neither the main effect of hand nor the Hand \times Movement Condition interaction reached significance. Post-t-tests revealed that only conditions MT and SC_{distant} differed from each other, $t(15) = 3.30, p < .01$. All other pairwise comparisons failed to reach significance. Furthermore, tests of within-subjects contrasts confirmed a strong linear trend, $F(5, 15) = 10.87, p < .01$, indicating a decrease of aiming bias that depends on the distance between target and manipulated square.

It is important to note, that the aiming bias does not merely depend on the distance between the actual target and the manipulated target per se. For conditions SC_{distant} and VV, these distances are exactly the same. However, in the posttest, the aiming bias significantly differed from zero in condition SC_{distant} ($M = +2.53$ mm, $SE = 1.09$ mm), $t(15) = 2.32, p < .05$, but not in condition VV ($M = +0.39$ mm, $SE = 0.78$ mm). Thus, the adaptation to the virtual displacement of a certain target seems to generalize only to movements in the same direction but not to

movements in the opposite direction. Moreover, this generalization decreases with the distance between the actual and the manipulated target.

Experiment 2

The intent of the second experiment was to examine whether the adaptation and transfer found in Experiment 1 depends upon the type of visual feedback in the exposure phase. For example, Cohen (1967) reported that prism aftereffects of the untrained limb only occur under terminal feedback but not when observers had continuous visual control of their movements when wearing the prismatic glasses. Like others before him, he suggested that continuous feedback would lead to a change in the felt position of the exposed arm (Harris, 1963), whereas terminal feedback would give rise to a re-interpretation of gaze direction which continues to influence movements after the prisms have been removed (e.g., Helmholtz, 1925, as cited in Cohen, 1967; Hamilton, 1964; Harris, 1965). On the basis of these assumptions, Canon (1970, 1971) proposed that conflicting spatial information from two (or more) modalities would preferably result in a recalibration of the modality that is actually less useful for spatial control. In case of terminal feedback, participants probably mainly rely on proprioception because visual feedback is scarcely provided. Thus, to overcome the intermodality conflict, vision would have to be adjusted to proprioception. In case of continuous feedback, however, participants presumably rely more on visual feedback and proprioception becomes adjusted to vision. Thus, one would expect reduced interlimb transfer in the case of continuous as compared to terminal feedback, as proprioception but not vision is specific to the exposed limb. Consequently, in the present experiment continuous feedback should lead to a reduced transfer of the acquired adaptation of the right hand to the left hand.

In our opinion, there is considerable reason to doubt Canon’s model. If visual and proprioceptive signals are actually combined to form a distributed representation of space (e.g., Brotchie et al., 1995; Andersen et al, 1997; Kalaska et al., 1997), then “adjustment of vision” and “adjustment of proprioception” can be regarded as being two sides of the same coin: learning a new mapping of vision-based target coordinates onto effector-based target coordinates. From this perspective, adapting to a visual displacement is not accomplished by a recalibration of either vision or proprioception but rather by recalibrating the relations between both. As a consequence, the amount of intermanual learning transfer should not depend on the type of feedback.

Continuous feedback might nevertheless affect the efficiency of adaptation. Learning in general is driven by the experience that certain goals are missed by a certain behavior. In this respect continuous feedback makes adaptation dispensable as the aiming movements can always be brought to success by on-line control. Participants might therefore rely on control by visual feedback instead of recalibrating the relations between the seen target locations and the coordinates of the to-be-performed hand movements. In line with this consideration Proteau, Marteniuk, Girouard, and Dugas (1987) found that intensive training of aiming movements under visual feedback enhances the use of visual feedback in movement execution instead of reducing it (cf. also

Elliott, Helsen, and Chua, 2001). Participants in the present experiment likewise might continuously improve the online control of their hand movements if visual feedback is continuously given so that there is not much need for a reinterpretation of target locations and accordingly a recalibration of target-movement assignments. However, if at least some recalibration takes place, it should become transferred to the untrained left hand.

Method

Participants

Thirty-two undergraduate students (22 females, 10 males) from the University of Würzburg, ranging in age from 19 to 34 years, participated in the study in fulfillment of a course requirement. All participants were right-handed, as determined by the Lateral Preference Inventory (Coren, 1993) and were naive as to the nature of the experiment.

Apparatus and Procedure

The apparatus and procedure were the same as in Experiment 1, except for the feedback conditions. During the exposure phase, we provided continuous visual feedback, that is, the position of the hand was continuously fed back by the blue spot no matter whether the stylus touched the tablet or not. Pretest and posttest phase remained unchanged.

Results and Discussion

Eight participants were excluded from data analysis. Four participants exceeded the time limit of 250 s for at least one of the blocks. Another four participants became aware of the manipulation and correctly named the manipulated target in the postexperimental interview.

Learning Process

Because of continuous visual feedback, participants always reached the respective targets during the exposure phase without additional corrective movements. Therefore, only PTs—not transversal aiming bias—indicated the learning progress. We analyzed PTs with a 6×4

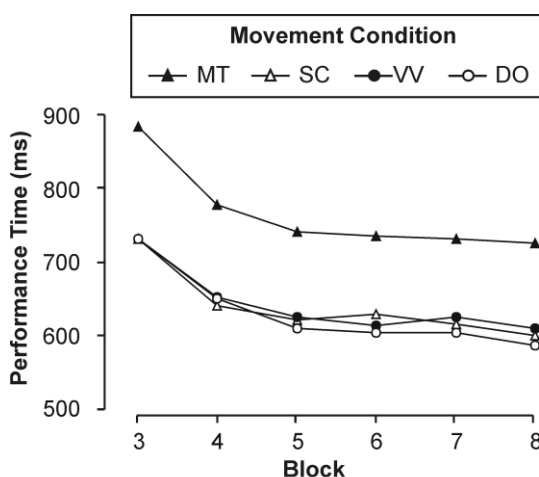


Figure 7. Mean performance time as a function of movement condition and block during the exposure phase in Experiment 2. The movement conditions were: MT (movements to the manipulated target) vs. SC (movements to a target in the same column as the manipulated target) vs. VV (movements to the target vis-à-vis of the manipulated target) vs. DO (movements to a target diagonally opposite the manipulated target).

(Block \times Movement Condition) ANOVA with repeated measures. Mean PTs are plotted in Fig. 7 as a function of movement condition and block.

We found a main effect of block, $F(1.41, 32.32) = 12.04$, $p < .001$, indicating an overall decrease of PT during the exposure phase. The mean time to reach the targets averages 769.33 ms ($SE = 42.62$ ms) in the third block but only 629.76 ms ($SE = 17.98$ ms) in the eighth block. This result clearly shows that learning has taken place. Furthermore, the results yielded a main effect of movement condition, $F(2.13, 46.96) = 32.34$, $p < .01$, but no significant Block \times Movement Condition interaction. Pairwise comparisons revealed that mean PT of condition MT ($M = 765.75$ ms, $SE = 18.87$ ms) was longer than that of any other condition was (SC: $M = 638.67$ ms, $SE = 20.96$ ms; VV: $M = 641.88$ ms, $SE = 25.57$ ms; DO: $M = 630.31$ ms, $SE = 25.47$ ms; $p < .001$ for all tests). The remaining comparisons failed to reach significance.

To assess the amount of additional programming effort, we examined PTs in every block with one-way analyses of covariance that controlled for movement length. None of the blocks yielded a significant main effect of movement condition. Therefore, longer PTs in condition MT cannot be attributed to additional programming effort. In contrast to Experiment 1, PTs simply reflect the increased movement length in condition MT. This result suggests that movement preparation—for example, determining an adequate movement length before movement initiation—may play a minor role when continuous visual feedback is available.

Learning transfer

To assess the amount of intermanual learning transfer we analyzed the pre-post-differences of the transversal aiming bias with a 2×4 (Hand \times Movement Condition) ANOVA with repeated measures. Mean pre-post-differences of the transversal aiming bias are depicted in Fig. 8 as a function of movement condition and hand.

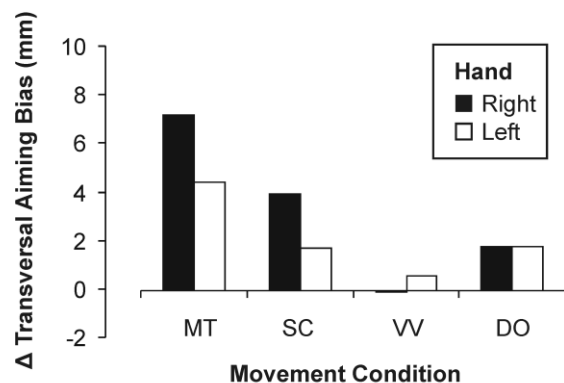


Figure 8. Mean pre-post-differences of transversal aiming bias as a function of hand (right vs. left) and movement condition (MT [movements to the manipulated target] vs. SC [movements to targets in the same column as the manipulated target] vs. VV [movements to the target vis-à-vis of the manipulated target] vs. DO [movements to targets diagonally opposite the manipulated target]) in Experiment 2. Only the right hand was trained during the exposure phase. Positive values indicate that movements to a certain target square had been longer in the posttest than in the pretest phase.

The results yielded a significant effect of movement condition, $F(1.68, 38.74) = 9.32$, $p < .001$. Participants showed the highest pre-post difference under condition MT ($M = +5.80$ mm, $SE = 1.43$ mm). Pairwise compari-

sions revealed that MT differed from all other movement conditions (SC: $M = +2.84$ mm, $SE = 1.38$ mm; VV: $M = +0.23$ mm, $SE = 1.02$ mm; DO: $M = +1.78$ mm, $SE = 0.84$ mm; $p < .05$, for all tests). In contrast to Experiment 1, we found no differences between any other two movement conditions. Furthermore, neither the main effect of hand, nor the Hand \times Movement Condition interaction reached significance.

These results indicate that intermanual learning transfer actually occurred under continuous feedback conditions. As in Experiment 1, movements to the manipulated target were larger than movements to other squares after exposure to the feedback manipulation, independently of whether they were made with the right or left hand. The amount of intermanual learning transfer (61.48 % in condition MT) seemed to be slightly smaller than in Experiment 1, however, the crucial Hand \times Movement Condition interaction failed to reach significance. Obviously, continuous feedback conditions do not preclude the transfer of an altered visuomotor mapping.

Generalization to Other Targets

In contrast to Experiment 1, we found no differences between conditions SC, VV, and DO in Experiment 2, as can be seen from the pairwise comparisons of the pre-post-test differences. Moreover, t-tests revealed that only the pre-post-difference in condition MT differed significantly from zero, $t(23) = 4.06$, $p < .01$. These results suggest that generalization did not take place under continuous feedback conditions. However, it is not clear whether generalization actually depends on the feedback condition. Adaptation might have been too weak for generalization to occur.

Comparison of intermanual transfer under terminal and continuous feedback

To directly compare the different feedback conditions, we analyzed pre-post-differences of the transversal aiming bias with a three-way ANOVA including hand (right vs. left) and movement condition (MT vs. SC vs. VV vs. DO) as within subject factors and feedback condition (terminal vs. continuous) as between subjects factor. Again, we found a highly significant main effect of movement condition, $F(1.76, 80.80) = 22.90$, $p < .001$. Pairwise comparisons revealed differences between all movement conditions ($p < .01$ for all tests), except between conditions VV and DO. Furthermore, there was a main effect of feedback condition, $F(1, 46) = 5.43$, $p < .05$, with higher pre-post-differences under terminal as opposed to continuous feedback conditions (terminal: $M = +6.05$ mm, $SE = 1.03$ mm; continuous: $M = +2.66$ mm, $SE = 1.03$ mm). All other tests failed to reach significance.

The main effect of feedback condition indicates that pre-post-differences of both hands were smaller under continuous as opposed to terminal feedback conditions. Obviously, adaptation to the visual displacement was impeded under continuous feedback. However, the kind of feedback did not affect the amount of intermanual learning transfer. Note that decreased intermanual learning transfer under continuous feedback conditions would have led to a significant Hand \times Movement Condition \times Feedback Condition interaction. This was apparently not the case. Instead, the left hand showed a pattern of pre-post-differences that strongly resembled to that of the right hand. Therefore, it seems reasonable to assume that

under both feedback conditions the adaptation to the virtual displacement of one target is due to a visuomotor re-mapping that can be transferred to the untrained hand.

General Discussion

The present study examined the adaptation of aiming movements to a virtual displacement of one of several targets and the transfer of this adaptation to the untrained hand. Participants trained aiming movements with their preferred right hand. During training they had no direct view of the hand. Instead, a virtual spot represented the position of the hand allowing a manipulation of visual feedback. The visual feedback was manipulated for movements to one selected target only. Movements to the manipulated target appeared shorter than they actually were. In order to prevent strategic adaptation to this manipulation, the virtual displacement of the critical target was withheld from the participants. We expected that participants would nevertheless adapt to the unnoticed virtual displacement by performing increasingly longer movements to the manipulated target.

Furthermore, we expected that adaptation would transfer to movements of the untrained left hand. We argued that movements of the untrained hand should show the same adaptation to the manipulated target as the trained hand, if the adaptation would be based on a "re-interpretation" of target locations on which both hands draw. In contrast, if adaptation would be based on muscle-specific motor commands, movements of the untrained hand to the target vis-à-vis of the manipulated target should be biased as they address muscles which are homologous to the adopted ones of the right hand.

The amount of adaptation and of intermanual transfer was assessed under terminal as well as under continuous visual feedback during training. We expected learning but not transfer to be impeded under continuous feedback. Furthermore, we addressed the question to what extent adaptation to the displacement of a single target would affect movements to adjacent non-manipulated targets.

Summary of results

The right hand adapted to the unnoticed target-specific visual displacement under terminal and continuous visual feedback. At the end of the exposure phase, larger movements were made to the manipulated target than to other targets. Adaptation was significantly more pronounced if participants received terminal as compared to continuous visual feedback. Moreover, under terminal feedback, adaptation to the manipulated target also affected movements to adjacent non-manipulated targets which required movements in the same direction. These movements were smaller than movements to the manipulated target, the more so the further away, but always larger than movements to targets in the opposite direction.

The adaptation of the right hand to the visual displacement was completely transferred to movements of the untrained left hand. The target specific pattern of pre-post-differences of the untrained left hand did not differ from the pattern showed by the trained right hand, irrespective of whether terminal or continuous visual feedback was given during training. Thus, both the trained and the untrained hand made larger movements to the

manipulated target and, under terminal feedback, to adjacent targets in the same direction.

Mechanisms of adaptation and transfer

The present results indicate that the adaptation of the right hand movements to the virtual displacement of a certain target was not based on muscle-specific motor commands. In this case, mirror reversed movements of the untrained left hand to targets vis-à-vis the manipulated target would have been affected, if at all, but never movements to the same targets which address muscles that are contradictory as compared to those which have adopted in the right hand. As the latter was clearly the case, an adaptation and transfer of muscle specific motor commands can be ruled out. We would rather assume that under the present condition the adaptation to the virtual displacement as well as its transfer to the other hand are based on a “re-interpretation” of the visual target locations on which the movement control of both hands draws.

An appropriate conceptualization of such a “re-interpretation” has to provide an account for all the three findings of the present experiments: First, it has to account for the fact that terminal feedback leads to a stronger adaptation of movement length than continuous feedback. Second, it has to account for the fact that under terminal feedback but not under continuous feedback movements to targets adjacent to the manipulated target are also affected. Third, the conceptualization has to account for the complete transfer of the adapted target specific movements to the untrained hand. Let us consider all three topics in turn:

Stronger adaptation under terminal than under continuous feedback

It is a plausible assumption that aimed movements are differently controlled under terminal and continuous visual feedback. The “classical” and still acknowledged two-component model of goal-directed movements (Woodworth, 1899; Elliott, Helsen, & Chua, 2001) distinguishes two movement phases, an initial impulse and subsequent corrective movements. According to the model, the initial impulse is a fast ballistic movement that serves to bring the limb into the vicinity of the target. In the second movement phase, visual feedback is used to guide the limb to the target position. As terminal feedback provides no visual information until the movement is finished, improvement of performance has to be a matter of adjusting the initial impulse rather than improving feedback control. Under continuous feedback, however, the adjustment of the initial impulse presumably plays a minor role for an improvement of performance as the actor can rely on visual feedback in order to bring the limb to the target.

In accordance with these considerations, Elliott, Carson, Goodman, and Chua (1991) found the initial component of aimed movements differently shaped in dependence on the availability of visual feedback. If visual feedback was provided during movement execution, participants spent more proportional time after peak velocity of the movement. Elliott et al. concluded that this extra time was used to process visual information in order to improve feedback control of the subsequent corrective movement. In a similar way, Khan, Coull, Chua, Lyons, & Elliott (2000, as cited by Elliott, Helsen,

& Chua, 2001) manipulated the availability of visual feedback between and within blocks. When participants could expect visual feedback to be continuously available, they spent significantly less time on movement preparation than they did under randomized feedback conditions or in ‘no-vision’ trials. These findings confirm the notion that under continuous visual feedback, participants rather rely on visual feedback instead of trying to improve the precision of the ballistic first component of the movement.

In the light of this evidence it seems reasonable to assume that in Experiment 1 in which only terminal feedback was provided, participants more strongly adjusted the parameters of the initial movement component to adapt to the virtually displaced location of the manipulated target than in Experiment 2 in which continuous visual feedback was provided. As Experiment 1 revealed significantly stronger adaptation to the virtual displacement, we conclude that the “re-interpretation” of target locations is to a substantially degree accomplished by assigning new parameters to the initial impulse to reach the manipulated target.

Transfer of target specific movement adaptation to movements in the same direction

We have found that under terminal feedback the adaptation to the displacement of one target was generalized to adjacent targets which require movements into the same direction. Interestingly, a similar pattern of generalization has been found for saccadic eye movements (Deubel, 1987; Miller, Anstis, & Templeton, 1981). For example, Deubel (1987) repeatedly displaced the target of a saccade during eye movement. Although the displacement was not noticed, saccades adapted to it. After adaptation, saccades to other locations were to be performed. Deubel found that the adapted saccade characteristics transferred to saccades which were to be performed into similar directions as the originally adapted saccade. The data suggested that this generalization is limited to an angular range of approximately 30° around the adapted direction. In accordance with this assumption, Hajos and Fey (1982) reported different adaptation rates to unnoticed target displacements for eye movements to the right and to the left, indicating that eye movements, at least to opposite directions, might adapt independently of each other.

As vision is blurred during a saccadic eye movement, saccades can be adjusted by the use of terminal feedback only. Thus, like the hand movements in Experiment 1, saccades can only adapt to a displacement of their targets by an adjustment of their parameters before initiation. As the findings of saccade adaptation to target displacements suggest that the adjustment of movement parameters occurs for movements in a certain direction, we assume that the parameters of the initial hand movements are not only assigned to a certain target but also to a certain movement direction. Consequently, the adapted parameters for the displaced target also transfer to other targets which require movements in the same direction as the adapted one. Under continuous feedback (Experiment 2) this transfer to adjacent targets is reduced as the adjustment of the initial movement to the displaced target is of reduced importance for adaptation here.

Transfer of target specific movement adaptation to the untrained hand

Our assumption that the adaptation of hand movements is mainly due to the acquisition of new parameters for the initial movements to the displaced target and targets in the same direction also provides an account for the transfer to the untrained hand. The assignment of parameters to a to-be-executed movement has been considered as being the formation of a motor program that allows the movement to be carried out uninfluenced by peripheral feedback (Keele, 1968). Furthermore, it has been argued that motor programs do not specify the parameters only for a certain movement of a certain effector but rather for movement sets irrespective of which effector is to be used to create the movement (e.g., Rosenbaum, 1980, 1985; Schmidt, 1975, 1988).

There is indeed ample evidence for such generalized motor programming. For example, Rosenbaum (1980, 1983) reported convincing evidence that the extent and the direction of required hand movements can be prepared in advance before the hand to be moved is specified. Likewise, the duration of a movement (e.g., Klapp, 1977) or its force (e.g., Zelaznik, 1981) can be pre-programmed before the effector is determined. Transfer studies also repeatedly showed that spatial and temporal characteristics of trained movements are transferred to untrained effectors (e.g., Grafton, Hazeltine, & Ivry, 1998; Teixeira, 2000; Viviani & Terzuolo, 1980), indicating that spatial and time parameters are represented apart from the concrete muscle commands, so that they can be used to control other movements as well.

In the light of this evidence, we assume that in the present experiments participants also acquire new parameters for the initial movements to the manipulated and adjacent targets which are not tightly coupled to the trained muscle-commands but are rather represented as abstract characteristics which can be transferred to movements of any limb. Consequently in the post-test, the movements of the untrained left hand are controlled by these parameters in the same way as the movements of the trained right hand, resulting in the same pattern of target-specific movement adaptations.

Final Conclusions

In order to account for the present data, we assume that the induced "re-interpretation" of target locations is accomplished mainly by the acquisition of new abstract parameters for initial movements to the visually given target locations which are used both for the control of right-hand and left-hand movements. In contrast, the mechanisms of visually controlled target approach are assumed to remain uninfluenced by the displacement.

Which parameters of the initial movements are affected is hard to say. It might be that participants incidentally learn to increase the force of the initial impulse for movements to the manipulated target (e.g., Teixeira, 2000). It might also be that participants incidentally adapt their anticipation of the landing point for movements to the manipulated target (e.g., Desmurget & CRAFTON, 2000). Finally, it might be that not single parameters become adjusted but rather a new inverse model is acquired in which several parameters of the goal oriented movements are intertwined with each other (e.g., Kalveram, 2002; Wolpert & Kawato, 1998). The present data do not allow to distinguish between these and possi-

bly further alternatives but they contribute to a refinement of the constraints which future models of motor adaptation to changed environmental conditions have to meet.

Although our data clearly speak against a transfer of muscle specific motor commands to homologous muscles of the contralateral hand, we do not want to completely exclude this possibility. For example, it is well known that demanding voluntary contractions in one limb (e.g., contractions under high force or fatigue) lead to a co-activation of the homologous muscles in the contralateral limb (e.g., Dimitrijevic, McKay, Sarajanovic, Sherwood, Svrtlih, & Vrbova, 1992; Zijdwind & Kernell, 2001). Likewise, Meyer, Roricht, Gräfin von Einsiedel, Kruggel, and Weindl (1995) found that cortically elicited motor responses of one hand were facilitated if strong contractions of the other hand were requested at the same time. As this also occurred in patients with an agenesis of the corpus callosum, Meyer et al. concluded that this effect takes place on a spinal rather than on a cortical level. The pyramidal tract might be a candidate system for the observed subcortical interactions (cf. also Gerloff et al., 1998; Spijkers et al., 2000; Cardoso de Oliveira, 2002). In fact, approximately 10 % of the pyramidal fibers remain uncrossed at the pyramidal decussation, descending in the ipsilateral corticospinal tract (Yakolev & Rakic, 1966). This corticospinal cross-talk presumably plays a decisive role in bimanual coordination, as Spijkers et al. (2000) have suggested, but it may also support interlimb transfer under special conditions.

However, if everyday life demands are considered, muscle specific representations of goal related movement requirements are completely inappropriate as every goal can and mostly has to be reached by a huge diversity of movements often of different limbs. For example, even a simple act like grasping an object should be as easily accomplished with the right as with the left hand, whichever hand is actually free. It appears reasonable to assume that intermanual learning transfer reflects this need to anticipate and control the consistent behavioral outcomes of the various movements to attain certain goals under permanently varying conditions. The fact that the incidental adaptation to a target-specific virtual displacement is not restricted to the motor output of the trained effector corroborates this consideration, because it ensures the success of goal-oriented movements even if another limb is to be used.

References

- Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, *20*, 303-330.
- Bedford, F. (1989). Constraints on learning new mappings between perceptual dimensions. *Journal of Experimental Psychology: Human Perception and Performance*, *15*, 232-248.
- Bray, C. W. (1928). Transfer of learning. *Journal of Experimental Psychology*, *11*, 443-467.
- Brotchie, P. R., Andersen, R. A., Snyder, L. H., & Goodman, S. J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. *Nature*, *375*, 232-235.
- Canon, L. K. (1970). Intermodality inconsistency of input and directed attention as determinants of the nature of adaptation. *Journal of Experimental Psychology*, *84*, 141-147.

- Canon, L. K. (1971). Directed attention and maladaptive "adaptation" to displacement of the visual field. *Journal of Experimental Psychology*, 88, 403-408.
- Cardoso de Oliveira, S. (2002). The neuronal basis of bimanual coordination: recent neurophysiological evidence and functional models. *Acta Psychologica*, 110, 139-159.
- Carlton (1979). Control processes in the production of discrete aiming responses. *Journal of Human Movement Studies*, 5, 115-124.
- Choe, C. S., & Welch, R. B. (1974). Variables affecting the intermanual transfer and decay of prism adaptation. *Journal of Experimental Psychology*, 102, 1076-1084.
- Cohen, M. M. (1967). Continuous versus terminal visual feedback in prism aftereffects. *Perceptual and Motor Skills*, 24, 1295-1302.
- Colby, C. L. (1998). Action-oriented spatial reference frames in cortex. *Neuron*, 20, 15-24.
- Coren, S. (1993). The lateral preference inventory for measurement of handedness, footedness, eyedness, and earedness: Norms for young adults. *Bulletin of the Psychonomic Society*, 31, 1-3.
- Desmurget, M., & Grafton, S. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Science*, 4, 423-431.
- Desmurget, M., Pélisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: Planning goal-directed movements. *Neuroscience and Biobehavioral Reviews*, 22, 761-788.
- Deubel, H. (1987). Adaptivity of gain and direction in oblique saccades. In J. K. O'Regan, & A. Lévy-Schoen (Eds.), *Eye movements: from physiology to cognition* (pp. 181-190). Amsterdam: Elsevier.
- Deubel, H. (1995). Separate adaptive mechanisms for the control of reactive and volitional saccadic eye movements. *Vision Research*, 35, 3529-3540.
- Dimitrijevic, M. R., McKay, W. B., Sarjanovic, I., Sherwood, A. M., Svrtlih, L., & Vrbova, G. (1992). Co-activation of ipsi- and contralateral muscle groups during contraction of ankle dorsiflexors. *Journal of Neurological Sciences*, 109, 49-55.
- Elliott, D., Carson, R. G., Goodman, D., & Chua, R. (1991). Discrete vs. continuous visual control of manual aiming. *Human Movement Science*, 10, 393-418.
- Elliott, D., Helsen, W. F., & Chua, R. (2001). A century later: Woodworth's (1899) two component Model of goal-directed aiming. *Psychological Bulletin*, 127, 342-357.
- Elliott, D., & Roy, E. A. (1981). Interlimb transfer after adaptation to visual displacement: patterns predicted from the functional closeness of limb neural control centres. *Perception*, 10, 383-389.
- Fechner, G. T. (1857). *Beobachtungen, welche zu beweisen scheinen, dass durch Übung der Glieder der einen Seite die der anderen zugleich mitgeübt werden* [Observations, which seem to prove, that through exercise of the limbs of one side, those of the other side are also trained at the same time]. Retrieved August 06, 2002, from Projekt Gutenberg-DE Web site: <http://Gutenberg.Spiegel.de/fechner/berichte/uebglied/uebglied.htm>.
- Fitts, P. M. (1954). The information capacity of the human motor system in controlling the amplitude of movement. *Journal of Experimental Psychology*, 46, 199-210.
- Gerloff, C., Cohen, L. G., Floeter, M. K., Chen, R., Corwell, B., & Hallett, M. (1998). Inhibitory influence of the ipsilateral motor cortex on responses to stimulation of the human cortex and pyramidal tract. *The Journal of Physiology*, 510, 249-259.
- Ghahramani, Z., & Wolpert, D. M. (1997). Modular decomposing in visuomotor learning. *Nature*, 386, 392-395.
- Grafton, S. T., Hazeltine, E., & Ivry, R. B. (1998). Abstract and effector-specific representations of motor sequences identified with PET. *Journal of Neuroscience*, 18, 9420-9428.
- Hajos, A., & Fey, D. A. (1982). Lernprozesse des okulomotorischen Systems [Learning processes of the oculomotor system]. *Psychologische Beiträge*, 24, 135-158.
- Hamilton, C. R. (1964). Intermanual transfer of adaptation to prisms. *American Journal of Psychology*, 77, 457-462.
- Harris, C. S. (1963). Adaptation to displaced vision: visual, motor or proprioceptive change? *Science*, 140, 812-813.
- Harris, C. S. (1965). Perceptual adaptation to inverted, reversed, and displaced vision. *Psychological Review*, 72, 419-444.
- Hellebrandt, F. A., Parrish, A. M., & Houtz, S. J. (1947). Cross education: the influence of unilateral exercise on the contralateral limb. *Archives of Physical Medicine*, 28, 76-84.
- Hicks, R. E., Gualtieri, C. T., & Schroeder, S. R. (1983). Cognitive and motor components of bilateral transfer. *American Journal of Psychology*, 96, 223-228.
- Imamizu, H., & Shimojo, S. (1995). The locus of visual-motor learning at the task or manipulator level: Implications from intermanual transfer. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 719-733.
- Imamizu, H., Uno, Y., & Kawato, M. (1995). Internal representations of the motor apparatus: Implications from generalization in visuomotor learning. *Journal of Experimental Psychology: Human Perception and Performance*, 21, 1174-1198.
- Imamizu, H., Uno, Y., & Kawato, M. (1998). Adaptive internal model of intrinsic kinematics involved in learning an aiming task. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 812-829.
- Kalaska, J. F., Scott, S. H., Cisek, P., & Sergio, L. E. (1997). Cortical control of reaching movements. *Current Opinion in Neurobiology*, 7, 849-859.
- Kalveram, K. T., & Schinauer, T. (2002). The problem of adaptive control in a living system or how to acquire an inverse model without external help. In: M. Verleysen (Ed.), *ESANN'2002 proceedings - European Symposium on Artificial Neural Networks* (pp. 89-94). Evere (Belgium): Mommaerts.
- Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, 70, 387-403.
- Klapp, S. T. (1977). Response programming, as assessed by reaction time, does not establish commands for particular muscles. *Journal of Motor Behavior*, 9, 301-312.
- Latash, M. L. (1999). Mirror writing: learning, transfer, and implications for internal inverse models. *Journal of Motor Behavior*, 31, 107-111.
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: psychophysical evidence for body-centered reference frames. *The Journal of Neuroscience*, 18, 8423-8435.
- Meyer, B. U., Roricht, S., Gräfin von Einsiedel, H., Kruggel, F., & Weindl, A. (1995). Inhibitory and excitatory interhemispheric transfers between motor cortical areas in normal humans and patients with abnormalities of the corpus callosum. *Brain*, 118, 429-440.
- Miller, J. M., Anstis, T., & Templeton, W. B. (1981). Saccadic plasticity: parametric adaptive control by retinal feedback. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 356-366.
- Prinz, W. (1992). Wahrnehmung [Perception]. In H. Spada (Ed.), *Allgemeine Psychologie* (pp. 25-114). Bern: Huber.
- Proteau, L., Marteniuk, R. G., Girouard, Y., & Dugas, C. (1987). On the type of information used to control and learn an aiming movement after moderate and extensive training. *Human Movement Science*, 6, 181-199.
- Rogosky, B. J., & Rosenbaum, D. A. (2000). Frames of reference for human perceptual-motor coordination: Space-based versus joint-based adaptation. *Journal of Motor Behavior*, 32, 297-304.
- Rosenbaum, D. A. (1980). Human movement initiation: Specification of arm, direction, and extent. *Journal of Experimental Psychology: General*, 109, 444-474.
- Rosenbaum, D. A. (1983). The movement precuing technique: Assumptions, applications, and extensions. In R. A. Magill (Ed.), *Memory and control of action* (pp. 231-274). Amsterdam: Elsevier.
- Rosenbaum, D. A. (1985). Motor Programming: A Review and Scheduling Theory. In H. Heuer, U. Kleinbeck, & K. H. Schmidt (Eds.), *Motor Behavior: Programming, Control, and Acquisition* (pp. 1-33). Berlin: Springer.
- Rosenbaum, D. A., Loukopoulos, L. D., Engelbrecht, S. E., Meulenbroek, R. G. J., & Vaughan, J. (1996). Integration of extrinsic and motor space. In T. Inui & J. L. McClelland (Eds.), *Attention and performance 16: Information integration in perception and communication* (pp. 315-333). Cambridge, MA: MIT Press.
- Saltzman, E. (1979). Levels of sensorimotor representation. *Journal of Mathematical Psychology*, 20, 91-163.

- Schmidt, R. A. (1988). *Motor control and learning* (2nd ed.). Champaign, Illinois: Human Kinetics.
- Spijkers, W., Heuer, H., Steglich, C., & Kleinsorge, T. (2000). Specification of movement amplitudes for the left and right hands: Evidence for transient parametric coupling from overlapping-task performance. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1091-1105.
- Stoddard, J., & Vaid, J. (1996). Asymmetries in intermanual transfer of maze learning in right- and left-handed adults. *Neuropsychologia*, *34*, 605-608.
- Teixeira, L. A. (2000). Timing and force components in bilateral transfer of learning. *Brain and Cognition*, *44*, 455-469.
- Thut, G., Cook, N. D., Regard, M., Leenders, K. L., Halsband, U., & Landis, T. (1996). Intermanual transfer of proximal and distal motor engrams in humans. *Experimental Brain Research*, *108*, 321-327.
- Uhlarik, J. J., & Canon, L. K. (1971). Influence of concurrent and terminal exposure conditions on the nature of perceptual adaptation. *Journal of Experimental Psychology*, *91*, 233-239.
- Vaughan, J., Rosenbaum, D. A., Harp, C. J., Loukopoulos, L.D., & Engelbrecht, S. (1998). Finding final postures. *Journal of Motor Behavior*, *30*, 273-284.
- Viviani, P. & Terzuolo, C. (1980). Space-time invariance in learned motor skills. In G. E. Stelmach & J. Requin (Eds.), *Tutorials in motor behavior* (pp. 525-533). Amsterdam: North-Holland.
- Willingham, D. B. (1999). The neural basis of motor-skill learning. *Current Directions in Psychological Science*, *8*, 178-182.
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Experimental Brain Research*, *103*, 460-470.
- Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*, 1317-1329.
- Woodworth, R. W. (1899). The accuracy of voluntary movement. *Psychological Review Monograph Supplement*, *3*, 1-114.
- Yakolev, P. I., & Rakic, P. (1966). Patterns of decussation of bulbar pyramids and distribution of pyramidal tracts on two sides of the spinal cord. *Transcripts of the American Neurological Association*, *91*, 366-367.
- Zelaznik, H. (1981). The effects of force and direction uncertainty on choice reaction time in an isometric force production task. *Journal of Motor Behavior*, *13*, 18-32.
- Zijdewind, I., & Kernell, D. (2001). Bilateral interactions during contractions of intrinsic hand muscles. *The Journal of Neurophysiology*, *85*, 1907-1913.