

Constraints on visuo-motor adaptation depend on the type of visual feedback during practice

Herbert Heuer · Mathias Hegele

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Abstract Adaptation to a novel visuo-motor gain has been found to generalize across target directions, whereas simultaneous adaptation to different direction-related visuo-motor gains turned out to be impossible. We ask whether this is a rigid constraint on human adaptability or a soft constraint that can be overcome by optimized conditions of practice. In particular, we compared practice with continuous visual feedback, as used in previous studies, to practice with terminal visual feedback. With terminal visual feedback only the final positions of the movements are shown. Both kinds of visual feedback in principle can serve the acquisition of an internal model of direction-related visuo-motor gains, but with continuous feedback on-line visual closed-loop control permits accurate movements without access to an internal model. Whereas we found no indication of visuo-motor adaptation after continuous-feedback practice, there was adaptation after terminal-feedback practice. This was revealed both by (direction-related) adaptive shifts of movement amplitudes in an open-loop test with cued visuo-motor transformation and by (direction-related) aftereffects in an open-loop test with absence of the visuo-motor transformation being cued. None of the two groups gave evidence of explicit knowledge of the direction-related visuo-motor gains. These findings show that constraints on human adaptability can depend on the kind of experience with visuo-motor transformations, in particular on the kind of feedback during practice.

Introduction

More than a 100 years of research have revealed a high degree of plasticity of human sensori-motor systems (for review, see Welch 1978). In the classic studies of adaptation the intrinsic relation between limb positions and their visual perception was distorted. In recent studies it was more frequently adaptation to an extrinsic relation between limb positions and visually perceived positions of a controlled object like a cursor on a computer monitor that was studied. An extrinsic relation between limb and object movement can be manipulated more easily than the relation between limb movements and their visual perception. In addition, modern technology creates an increasing number of workplaces in which the consequences of hand movements indeed are observed on a monitor. Thus, exploration of the constraints on visuo-motor plasticity is no longer only of theoretical, but also of practical interest.

Movements can be described in terms of amplitude and direction. There is evidence that these parameters are also involved in planning and control (cf. Gordon et al. 1994; Rossetti et al. 1995; Vindras and Viviani 1998, 2002; Vindras et al. 2005). Thus, it is important to explore adaptation to both variations of the visuo-motor gain, that is, variations of the ratio of the amplitudes of cursor motion and the associated hand movement, and visuo-motor rotations, that is, differences between the directions of cursor motion and the associated hand movement. These two types of adaptation have been shown to have different characteristics (e.g., Krakauer et al. 2000) as well as different neural substrates (e.g., Krakauer et al. 2004). Moreover, adaptation to a novel visuo-motor gain not only generalizes across amplitudes, but also across directions (Bock 1992; Heuer and Hegele 2007; Krakauer et al. 2000; Vindras and Viviani 2002). More important, Bock (1992)

H. Heuer (✉) · M. Hegele
Institut für Arbeitsphysiologie an der Universität Dortmund,
Ardeystraße 67, 44139 Dortmund, Germany
e-mail: heuer@ifado.de

observed that adaptation to direction-related visuo-motor gains was approximated by a single gain factor that was independent of direction.

The present study serves to examine the robustness of Bock's (1992) observation of lack of adaptation to direction-related visuo-motor gains. In particular we inquire about the role of different types of visual feedback during practice. Bock (1992) used continuous visual feedback. A visible cursor displayed the (transformed) position of the hand during each movement so that visual closed-loop control was possible. Both experimental data and theoretical considerations suggest that terminal visual feedback might be more effective than continuous visual feedback in inducing adaptation to certain extrinsic visuo-motor transformations. With terminal visual feedback the cursor is presented only at the end of the movement. Thus, the error at the end of the movement is displayed, but on-line corrections based on visual feedback are impossible.

On one hand, adaptation has been found after practice with continuous visual feedback in numerous studies. In fact, there are certain extrinsic visuo-motor transformations for which adaptation might even depend on the continuous presence of visual feedback. In particular, these are transformations which transform a straight hand movement into a curved path of the cursor, and for which adaptation results in a straight path of the cursor and a curved trajectory of the hand (e.g., Flanagan and Rao 1995; Goodbody and Wolpert 1999; Wolpert et al. 1995). On the other hand, there are also transformations for which adaptation requires terminal visual feedback. For example, for a rather small visuo-motor rotation, which participants were not consciously aware of, Bernier et al. (2005) observed adaptation with terminal, but not with continuous visual feedback. Thus, at least for certain kinds of extrinsic visuo-motor transformations, adaptation might be better with terminal than with continuous visual feedback, and for adaptation to direction-related visuo-motor gains terminal visual feedback could be a prerequisite.

Turning to theoretical considerations, mastery of an extrinsic visuo-motor transformation requires that it be inverted to determine the input that results in a desired output. The inversion can be achieved in two different ways (cf. Jordan 1996). The first one is visual closed-loop control. (Note that we deal with transformations the output of which can be only visually perceived.) The second possibility is visual open-loop control which includes an (inverse) internal model of the extrinsic visuo-motor transformation. The role of both the mechanisms is illustrated in a study of Davidson et al. (2000). In a tracking task, they observed improvement of performance with two different visuo-motor transformations under visual closed-loop conditions. However, in open-loop tests an improvement was seen with only one of the transformations. Such a

pattern of results suggests an improvement of closed-loop processes during practice with both transformations, but the acquisition of an internal model for only one of them.

When visual feedback is available, an extrinsic visuo-motor transformation can generally be mastered, so that there is no need to acquire an internal model (cf. Smeets et al. 2006). During prolonged practice, performance can even become dependent on visual feedback (e.g., Proteau et al. 1987, 1992; Proteau and Isabelle 2002). In contrast, without visual feedback accurate performance can only be achieved when a sufficiently accurate internal model of the visuo-motor transformation has been acquired. Thus, the absence of continuous visual feedback can serve to more or less enforce the acquisition of internal models of visuo-motor transformations, for which terminal visual feedback provides the necessary information.

The adaptive changes seen under visual open-loop conditions are generally attributed to an internal model of the visuo-motor transformation. However, in addition, there may be strategic corrections. Here we conceive of strategic corrections as being based on explicit knowledge. Whereas an internal model establishes new visuo-motor relations, strategic corrections are thought to be based on intentional changes of movement characteristics. For example, one can point to a location that is farther or nearer than the location of the visual target. After effects are generally thought of as measures of adaptation, which are unconfounded by strategic corrections. In the present study, therefore, we used not only open-loop tests with the presence of the transformation being cued, but also open-loop tests with cued absence of the visuo-motor transformation to assess the after effects. In addition we collected explicit judgments of the movement amplitudes appropriate to reach the visual targets in the presence of the visuo-motor transformation. Finally, we added a visual closed-loop test and an extended period of visual open-loop performance.

Methods

Participants

Two groups of participants, a continuous-feedback group and a terminal-feedback group, took part in the experiment. Participants were assigned to groups alternately in their order of recruitment. The continuous-feedback group consisted of 11 women and 5 men, aged 21–29 years (mean 25.0 years; SD 2.85 years). The terminal-feedback group consisted of ten women and six men, aged 20–30 years (mean 24.7 years; SD 2.50 years). All participants were self-declared right-handers with normal color vision according to the Ishihara test. Most of them were students of Dortmund University and were paid for their

participation or received course credit. All participants had given informed consent prior to the start of the experiment that was done in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Apparatus

Participants sat on a height-adjustable chair. They faced a 15-in. LCD monitor (EIZO FlexScan L365) in about 100 cm distance from their eyes. Between the monitor and the participants a glass plate was placed on the table on which the movements were performed. The right index finger of the participants was strapped to a slide of $50 \times 30 \text{ mm}^2$ (6 mm height), which ran on the glass plate with only a little friction. Directly above the finger nail the slide carried a vertically oriented sensor of a miniBIRD 800 system (Ascension Technology Corporation, Burlington, VT, USA). The position of the finger was recorded at 103.6 Hz (spatial resolution: 0.11 mm). An occluder 20 cm above the table platform prevented vision of the hand. To assist in finding the start location, a disc of 4 mm height and 13 mm diameter was placed on the glass plate. The start location was just in front of this disk.

Task

Participants performed aimed movements from a common start location to targets in different directions, ranging from 0° (to the right) to 90° (forward). They were instructed to move swiftly and as accurately as possible (in German: “zügig und so genau wie möglich”). Continuous or terminal visual feedback was provided by means of a cursor on the monitor. Participants were instructed that there were trials with and without a novel visuo-motor transformation in the experiment, but the nature of the transformation was not explained. The absence or presence of the transformation was cued by the color of the circle, which marked the start location, either green or red, respectively.

In the absence of the transformation the amplitude of the cursor motion was the same as the amplitude of the hand movement, $a_c = a_h$. Thus, the visuomotor gain was $g = 1.0$. In the presence of the transformation, the visuomotor gain varied across movement directions. The direction-related visuo-motor gain was

$$g(\theta) = \frac{0.75 \times 1.25}{\sqrt{1.25^2 \sin^2 \theta + 0.75^2 \cos^2 \theta}}. \quad (1)$$

Thus the amplitude of cursor motion was $a_c = g(\theta) \times a_h$, and the amplitude of hand movement appropriate for a desired visual amplitude a_c^* was $a_h = \frac{1}{g(\theta)} a_c^*$. In Table 1 the correct hand-movement amplitudes for the visual target amplitudes used in the experiment are given, also the errors of the amplitudes of cursor motion under the assumption that the hand amplitudes match the visual target amplitudes.

In practice trials target directions were 0° , 22.5° , 45° , 67.5° , and 90° , target amplitude was 80 mm; in test trials target directions were 0° , 34° , and 90° with target amplitudes of 40, 80, and 120 mm. In practice trials the direction-related visuo-motor gains were 1.25, 1.11, 0.91, 0.79, and 0.75 for the five target directions, and in test trials they were 1.25, 1.00, and 0.75. In test trials a smaller number of target directions was used than in practice trials to allow an examination of transfer to unpracticed target amplitudes within sufficiently short blocks of visual open-loop trials.

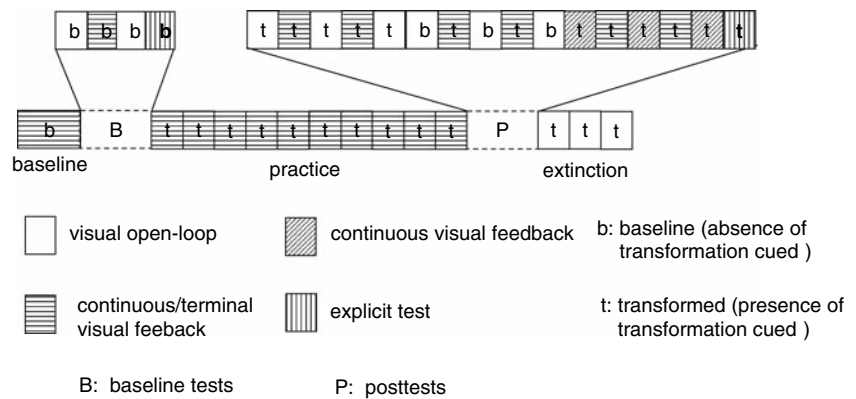
Design and procedure

The various phases of the experiment are shown in Fig. 1. A series of baseline practice trials was followed by the baseline tests. After the practice phase the post-tests followed and an extinction phase. Practice blocks and extinction blocks consisted of 25 trials each, with the five target directions presented in a pseudorandom order. The initial baseline practice consisted of six repetitions of the

Table 1 Correct amplitudes of hand movements for different target amplitudes and target directions, $a_h(a_c^*)$, and amplitude errors of cursor motions when amplitude of hand movements match the visual target amplitudes, $a_c(a_h = a_c^*) - a_c^*$

Target direction	$a_h(a_c^*)$ target amplitude (mm)			$a_c(a_h = a_c^*) - a_c^*$ target amplitude (mm)		
	40	80	120	40	80	120
0°	32.0	64.0	96.0	+10.0	+20.0	+30.0
22.5°	–	71.8	–	–	+9.1	–
34.0°	39.9	79.8	119.7	+0.1	+0.2	+0.3
45.0°	–	88.0	–	–	–7.2	–
67.5°	–	101.5	–	–	–17.0	–
90.0°	53.3	106.7	160.0	–10.0	–20.0	–30.0

Fig. 1 Sequence of the phases of the experiment



set of five target directions (with different pseudorandom orders). Visual feedback in the baseline blocks and practice blocks was continuous or terminal, depending on experimental group, and it was absent in the extinction blocks.

Test blocks consisted of nine trials each, with each combination of three target directions and three target amplitudes being presented once in a pseudorandom order. In-between test blocks maintenance blocks of five trials were inserted, which were identical to practice blocks except for the number of trials. The baseline tests consisted of two blocks of open-loop trials and a block of explicit trials; in all trials the absence of the visuo-motor transformation was cued by the green color of the start circle. The post-tests consisted of three blocks of open-loop trials with the presence of the transformation being cued (red color of the start circle), three blocks of open-loop trials with the absence of the transformation being cued (green color of the start circle), three blocks of trials with continuous visual feedback, and a single block of explicit trials.

Each movement trial started with the presentation of the start circle (outline circle of 7.6 mm diameter). The cursor (filled cyan circle of 4.6 mm diameter) was presented in the vicinity of the start circle to give some guidance in homing-in on the start position. During homing-in the visuo-motor gain was one in all trials. After a randomly chosen period of 500, 700, 900, 1,100, or 1,300 ms, during which the finger had to remain in the start location, a target was presented (filled white circle of 5.3 mm diameter). At the same time the start circle disappeared, and in open-loop trials and terminal-feedback trials the cursor disappeared as well. The on-line criterion for the end of the movement required that the distance between successively sampled positions was not larger than 0.16 mm for more than 400 ms. In closed-loop trials with continuous visual feedback the cursor had to be within a tolerance range of 2.7 mm around the target location in addition. When the movement had ended, the target disappeared in open-loop trials, and in closed-loop trials with continuous visual

feedback target and cursor disappeared. In closed-loop trials with terminal visual feedback the cursor reappeared and was presented in its final position for 1,000 ms, together with the target.

In the explicit tests each trial began with the presentation of the start circle, a target, and a white line of 2.3 mm width. It was parallel to the imaginary line connecting start and target, but shifted upward or to the left by 11 mm. The experimenter increased its length by way of pressing a key, beginning at zero length. The task of the participant was to instruct the experimenter to increase or decrease the length of the line until it matched the amplitude of the hand movement he or she thought appropriate to move the cursor from the start circle to the target circle.

Data analysis

For each trial the x and y positions both of the finger on the table and the cursor on the monitor were low-pass filtered (fourth-order Butterworth, 10 Hz, dual pass) and differentiated (two-point central difference algorithm). The start and end of each movement were determined from the tangential velocity of the finger, without taking accuracy into account. Starting at peak tangential velocity, both in a forward and a backward search those samples were determined at which tangential velocity became smaller than 5 mm/s for at least 200 ms. Movements with extreme durations (<200 ms or >5,000 ms) as well as movements with extremely long trajectories (longer than five times the distance between initial and final hand position) were excluded from further analyses. In total these were 9 of 6,784 trials (0.13%) in the continuous-feedback group and 4 of 6,784 trials (0.06%) in the terminal-feedback group.

Practice trials, extinction trials, and trials of the closed-loop test were analyzed in terms of amplitude error and movement time. For the practice trials and the extinction trials medians were computed for each target direction and each block of trials. For the visual closed-loop test medians

were computed for each of the nine combinations of target directions and target amplitudes. For the open-loop tests and the explicit tests amplitudes of hand movements were analyzed. Medians were computed again for each combination of three target directions and three target amplitudes, except for the explicit tests, in which each target was presented only once. Medians were used because they are less influenced than means by remaining extreme values of the dependent variables in individual trials.

The individual medians of amplitude errors, movement times, and amplitudes of hand movements were analyzed by means of a series of ANOVAs. In addition to the between-participant factor feedback-group and the relevant within-participant factors, the between-participant factor gender was included. However, this only served to give equal weights to the male and female subgroups and thus to avoid biasing of the differences between feedback groups by the slightly different proportions of male and female participants.

Results

The results will be reported for the various phases of the experiment in turn; first for the practice phase, second for the pretest-to-post-test changes, third for the closed-loop test, and the fourth for the extinction phase.

Practice phase

In Fig. 2 the mean errors in the practice phase are shown for the terminal-feedback group. Initially overshoots were

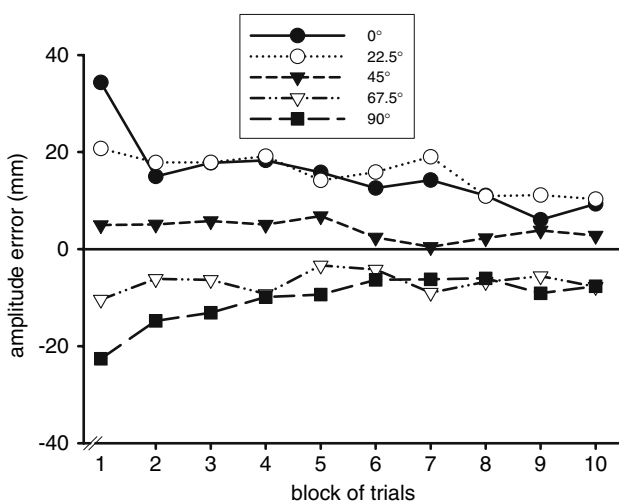


Fig. 2 Mean error of cursor amplitude during practice of the terminal-feedback group as a function of target direction and block of trials

strongest for those directions (0° , 22.5°) for which visuo-motor gains were largest (1.25, 1.11), whereas for those directions (67.5° , 90°) for which visuo-motor gains were smallest (0.79, 0.75) amplitude errors were undershoots. In the continuous-feedback group mean amplitude errors hardly deviated from zero and are not shown in Fig. 2. In spite of their small size, however, they turned systematically into longer undershoots as the target direction changed from 0° to 90° , being -0.1 mm for 0° and -1.2 mm for 90° . A four-way ANOVA with the between-participant factors feedback group and gender and the within-participant factors target direction and block of trials revealed a significant interaction of group and target direction, $F(4, 112) = 38.4$, $P < 0.01$. In separate analyses for the two groups the main effect of target direction was not only significant for the terminal-feedback group, $F(4, 56) = 43.5$, $P < 0.01$, but also for the continuous-feedback group, $F(4, 56) = 14.2$, $P < 0.01$. In the terminal-feedback group amplitude errors were mainly overshoots, but in the continuous-feedback group they were undershoots; the difference was significant, $F(1, 28) = 4.5$, $P < 0.05$.

As shown in Fig. 2, in the terminal-feedback group both overshoots and undershoots declined in the course of practice without vanishing completely. This convergence of errors was absent in the continuous-feedback group. The interaction among feedback group, target direction, and block was significant, $F(36, 1,008) = 5.0$, $P < 0.01$. In separate analyses for the two groups the interaction between target direction and block was significant only for the terminal-feedback group, $F(36, 504) = 5.3$, $P < 0.01$. From Fig. 2 it is obvious that the differences between the target directions of 0 and 22.5° as well as between the target directions of 67.5° and 90° disappeared rather early in practice. Thus, the rate of adjustment was faster for stronger deviations of the visuo-motor gain from one than for smaller deviations.

The mean movement times in the practice phase are shown in Fig. 3. In the course of practice, movement times declined overall, $F(9, 252) = 6.0$, $P < 0.01$, and in the continuous-feedback group they were longer than in the terminal-feedback group, $F(1, 28) = 12.6$, $P < 0.01$. Only in the continuous-feedback group there was a pronounced difference between movements with different target directions (and different visuo-motor gains) which was reduced in the course of practice. The interaction of feedback group and target direction was significant, $F(4, 112) = 14.8$, $P < 0.01$, as was the interaction of feedback group, target direction, and block, $F(36, 1,008) = 1.6$, $P < 0.05$. In separate analyses for the two groups the main effect of target direction and the target direction \times block interaction were significant only for the continuous-feedback group, $F(4, 56) = 63.2$, $P < 0.01$, and $F(36, 504) = 1.9$, $P < 0.01$, respectively.

Adaptive changes and aftereffects

Adaptive changes and aftereffects are defined by post-test minus baseline-test differences of the amplitudes of hand movements. In the tests with cued visuo-motor transformation these differences are adaptive changes,¹ in the tests without transformation they are aftereffects. Adaptive changes were determined both for open-loop amplitudes and explicit judgments.

For the target direction of 34°, for which the visuo-motor gain with cued transformation was 1.0, no adaptive changes would be expected. For the target direction of 0°, for which the visuo-motor gain had been 1.25 during practice, movement amplitudes should be reduced in the post-test, and they should be increased for the target direction of 90°, for which the visuo-motor gain had been 0.75. Both the increase and the reduction should be the stronger the larger the target amplitude is. The ideal adaptive changes are illustrated in Fig. 4a. Of course, the observed adaptive changes will be less than perfect, and the pattern will be deformed by variations of movement amplitudes in the course of the experiment which are unrelated to adaptation. However, such imperfections should leave the two core characteristics of Fig. 4a unaffected, namely the gradation of the adaptive shifts according to target directions, and thus according to the direction-related visuo-motor gains, and the divergence of shifts at different target directions with increasing target amplitude.

For the statistical analysis of the adaptive changes and aftereffects we ran a series of ANOVAs, separately for each type of test and each feedback group, with the focus on the main effects of target direction and the interactions of target direction and amplitude. These effects capture the core characteristics of the expected results (Fig. 4a). As is evident from Fig. 4d, for the explicit judgments neither the main effect of target direction nor the interaction of target

¹ Typical measures in studies of adaptation to novel visuo-motor transformations are errors, which are gradually reduced in the course of practice, and aftereffects, which can be observed in the absence of the transformation. Aftereffects are “negative” relative to the errors that are induced by the transformation. Measures of adaptive changes, as we use them, are uncommon. They are equivalent to aftereffects in that they are “negative.” Aftereffects can be conceived as components of adaptive changes which persist in spite of the knowledge that the novel visuo-motor transformation is no longer in effect. Both adaptive changes and aftereffects are direct measures of the changes of the movements produced rather than of the effects of these changes on the output of the visuo-motor transformation. Nevertheless, adaptive changes can also be expressed in terms of cursor amplitude: for a given visuo-motor gain they are proportional to the difference between post-test amplitude and baseline-test amplitude multiplied by the gain. This again is the difference between post-test amplitude and the expected post-test amplitude in the absence of any adjustment to the novel visuo-motor gain.

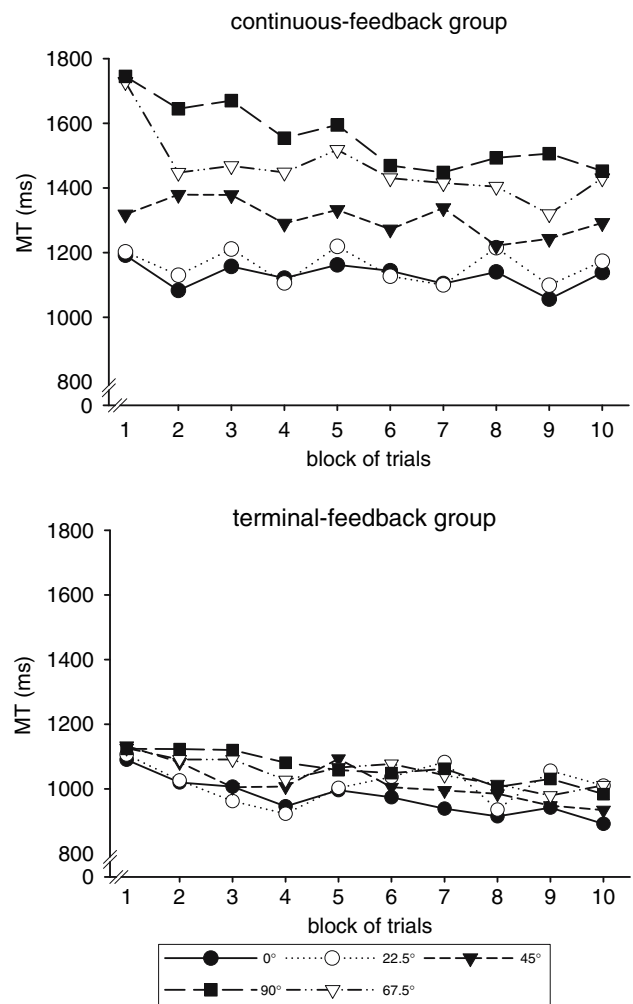


Fig. 3 Mean movement time during practice of the continuous-feedback group and the terminal-feedback group as a function of target direction and block of trials

direction and target amplitude approached significance in either of the two experimental groups.

In the continuous-feedback group the main effect of target direction was significant both for the adaptive shift, $F(2, 28) = 9.1$, $P < 0.01$, and for the aftereffect, $F(2, 28) = 7.5$, $P < 0.01$. However, the gradation of the adaptive shifts and aftereffects by the three target directions was not appropriate for adaptation to the direction-related visuo-motor gain (Fig. 4b, c). In addition the interactions of target direction and target amplitude failed to reach statistical significance, $F(4, 56) = 2.2$, $P < 0.10$, and $F(4, 56) = 1.6$, $P > 0.10$, respectively.

For the terminal-feedback group the gradation of adaptive shifts and aftereffects by target direction was the appropriate one (Fig. 4b, c). The main effects of target direction were significant, $F(2, 28) = 26.1$, $P < 0.01$, and $F(2, 28) = 11.3$, $P < 0.01$, respectively. In addition the interactions of target direction and target amplitude were

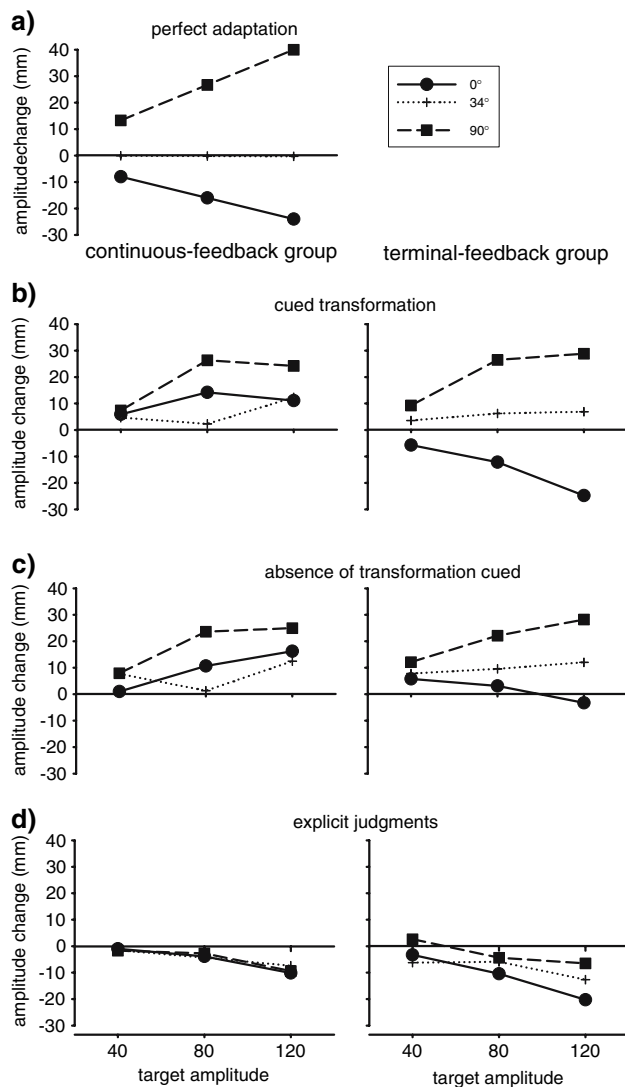


Fig. 4 Pretest-to-post-test changes of hand amplitude as a function of target amplitude and target direction. **a** Expected changes in the case of perfect adaptation (for the direction of 34° no change was expected), **b** observed changes in the open-loop test with transformation (adaptive changes) in the continuous-feedback group and the terminal-feedback group, **c** observed changes in the open-loop test without transformation (aftereffects) in the continuous-feedback group and the terminal-feedback group, and **d** observed changes in the explicit test with transformation (adaptive changes of explicit judgment) in the continuous-feedback group and the terminal-feedback group

significant, $F(4, 56) = 10.3$, $P < 0.01$, and $F(4, 56) = 4.1$, $P < 0.01$.

A second set of ANOVAs included the factor feedback group. Here the main interest was in group differences. For the adaptive shift (Fig. 4b) the three-way interaction of group, target direction, and target amplitude was almost significant, $F(4, 112) = 2.4$, $P < 0.06$. Reflecting the incorrect order of adaptive shifts across target directions after practice with continuous visual feedback, but not after

practice with terminal visual feedback, the interaction of group and target direction was significant, $F(2, 56) = 12.4$, $P < 0.01$. For the aftereffects (Fig. 4c) the three-way interaction of group, target direction, and target amplitude, only approached significance, $F(4, 112) = 2.0$, $P < 0.10$, and so did the interaction of group and target direction, $F(2, 56) = 2.4$, $P < 0.11$.

Continuous-feedback test

Amplitude errors in the continuous-feedback test were necessarily small and did not differ between the two feedback groups. However, as in the practice phase, they depended systematically on target direction and the associated visuo-motor gain, being -0.2 , -0.1 , and -1.1 mm for target directions of 0° , 34° , and 90° . An ANOVA with the between-participant factors feedback group and gender and the within-participant factors target direction and target amplitude revealed the effect of target direction to be significant, $F(2, 56) = 13.2$, $P < 0.01$.

Movement time in the terminal-feedback group was somewhat longer than in the continuous-feedback group, 1,404 ms vs. 1,287 ms, but this difference failed to reach statistical significance, $F(1, 28) = 2.1$, $P < 0.20$. The group difference was smallest for the 0° target direction, 1,190 ms vs. 1,142 ms, larger for the 34° target direction, 1,326 ms vs. 1,225 ms, and largest for the 90° target direction, 1,696 ms vs. 1,495 ms. However, the interaction of feedback group and target direction failed to reach statistical significance as well, $F(2, 56) = 2.2$, $P < 0.20$. The increase of movement time across the target directions of 0° , 34° , and 90° (1,166, 1,275, and 1,596 ms) was significant, $F(2, 56) = 70.9$, $P < 0.01$, and so was its increase with target amplitude, $F(2, 56) = 120.4$, $P < 0.01$, 1,050, 1,359, and 1,628 ms for target amplitudes of 40, 80, and 120 mm.

Extinction phase

Movement time in the extinction phase was 891 ms overall, and there was no significant variation across groups, target directions, and blocks of trials. Amplitude errors (of the invisible cursor) were 76, 66, 45, 23, and 13 mm in the continuous-feedback group for the target directions of 0° , 22.5° , 45° , 67.5° , and 90° , and in the terminal-feedback group they were 26, 24, 13, 4, and 2 mm. Both the main effect of feedback group, $F(1, 28) = 8.1$, $P < 0.01$, and the interaction of group and target direction, $F(4, 112) = 11.1$, $P < 0.01$, were significant. Only in the terminal-feedback group the amplitude of hand movements varied across target directions, 85, 91, 99, 104, and 109 mm. This

variation partially compensated the effects of the variation of the visuo-motor gain. In contrast, in the continuous-feedback group the amplitude of hand movements was independent of target direction, 127, 124, 125, 124, and 124 mm.

Amplitude errors were not only larger in the continuous-feedback group than in the terminal-feedback group, but they also increased across the three blocks of extinction trials, and the differences between target directions became larger. Both these changes across blocks of trials were absent in the continuous-feedback group. The interaction of group and block was significant, $F(2, 56) = 5.9$, $P < 0.01$, and so was the interaction of group, block, and target direction, $F(8, 224) = 2.3$, $P < 0.05$.

Discussion

Human sensori-motor systems are distinguished by their adaptability. Nevertheless there are limitations which point to the existence of certain constraints (cf. Bedford 1989; Bock 1992). The purpose of the present study was to examine the generality of one of the possible constraints, namely the direction-independence of adaptation to novel visuo-motor gains (Bock 1992). Whereas we replicated Bock's (1992) failure to observe adaptation to direction-related visuo-motor gains when visual feedback during practice was continuous, we observed both appropriate adaptive changes and aftereffects when terminal visual feedback was provided during practice, and these adaptive changes persisted throughout a rather long sequence of visual open-loop trials.

The present results can be conceived as a particular instance of the specificity of practice (cf. Proteau et al. 1992). Practice without on-line visual feedback resulted in learning that revealed its benefits in situations in which no on-line visual feedback was available. However, practice with continuous visual feedback resulted in no particular advantages in tests with continuous visual feedback, neither in terms of accuracy nor in terms of movement time. This was the case even though during practice movement time was considerably longer with continuous than with terminal visual feedback, suggesting that the on-line processing of visual feedback was time consuming.

Even though the present results give no evidence of an improvement of closed-loop processes after practice with continuous visual feedback, they do not justify the conclusion that such an improvement does not exist. First, the lack of evidence consists in the absence of a statistically significant difference between the two experimental groups, even though in the test with continuous visual feedback the continuous-feedback group had a movement-time advantage of 117 ms. Second, only with terminal

visual feedback an internal model of the visuo-motor transformation was acquired. Therefore, the remaining movement errors to be nullified by visual closed-loop control became smaller in the course of practice. This was not the case in the continuous-feedback group. The difference between groups with respect to the load on feedback-based corrections may have masked an eventual difference with respect to the efficiency of the processing of visual feedback. Consistent with such a conclusion, we have observed faster movement times in a test with continuous visual feedback after practice with continuous visual feedback than after practice with terminal visual feedback when no appropriate internal model of the visuo-motor transformation was acquired (Heuer and Hegele, in press).

The present findings revealed no explicit knowledge of the direction-related visuo-motor gains, neither after continuous-feedback practice nor after terminal-feedback practice. Thus, the different effects of the two kinds of visual feedback on adaptation cannot be attributed to differences with respect to strategic corrections based on explicit knowledge of the correct movements. In line with this conclusion, the difference between the two feedback groups was seen not only in the adaptive shifts, but also in the aftereffects.

The absence of explicit knowledge in the terminal-feedback group is remarkable for the following reason. With terminal visual feedback the deviation of the amplitude of cursor motion from the amplitude of hand movement is clearly presented at the end of each trial. Even when an internal model has been partially acquired, the cursor locations presented should deviate from the expected locations. Such unexpected events have been posited to trigger conscious search for their causes, so that they should give rise to conscious awareness of the relation between the amplitudes of hand movements and cursor motions (cf. Frensch et al. 2002; Haider and Frensch 2005). The present data do not support this hypothesis.

Bock's (1992) finding of essentially no adaptation to direction-related visuo-motor gains is consistent with the notion that direction and amplitude are separate parameters of motor planning and control (e.g., Gordon et al. 1994; Rossetti et al. 1995; Vindras et al. 2005), which are associated with distinct mechanisms of adaptation (Krakauer et al. 2000, 2004). According to the present findings, however, adaptation to direction-related visuo-motor gains is absent only with continuous visual feedback during practice, but present with terminal visual feedback. The latter finding, then, is consistent with direction-selective channels of the arm motor system (cf. Bock 1992). Taken together, the findings suggest that direction-selective channels of amplitude control do exist, but that there is a default mode of adjusting visuo-motor gains uniformly

across all channels. Deviations from this default mode can be triggered by appropriate environmental circumstances, for example movement errors that cannot be reduced otherwise. This is exactly what terminal visual feedback effects during practice.

In contrast to the present findings as well as those of Bernier et al. (2005), in studies of prism adaptation it is the type of adaptive change, but not its size, which depends on the kind of visual feedback. Cohen (1967, 1974) observed intermanual transfer of adaptation of pointing to visual and auditory targets after practice with terminal visual feedback, but not after practice with continuous visual feedback. The conclusion from these results is that continuous visual feedback leads to an adaptive change of felt arm position, but terminal visual feedback to a change of visual direction, as shown more directly, e.g., by Uhlarik and Canon (1971) and Redding and Wallace (1990). According to Uhlarik and Canon (1971), with continuous visual feedback attention is focussed on visual information during movement execution, but with terminal visual feedback on kinaesthetic information. Under this hypothesis the results are consistent with findings obtained when the attentional focus was varied by means of instruction: it is primarily the non-attended modality that exhibits an adaptive change (Canon 1970, 1971; Kelso et al. 1975).

At present it is not clear why the effects of the type of visual feedback during practice are different for adaptation to prismatically induced lateral displacement and for adaptation to an extrinsic visuo-motor transformation. The adaptive processes in these two types of situation are certainly different (e.g., Bedford 1993, 1995; Clower and Boussaoud 2000; Welch 1972), but this does not necessarily imply that different mechanisms are involved. Perhaps the relevant differences are related to the fact that with prismatic displacement, but not with an extrinsic visuo-motor transformation, there is a discrepancy between location signals provided by different sensory modalities. In one situation visual and kinaesthetic location information refer to the same object, the hand, but in the other situation they refer to different objects, the cursor and the hand, respectively. Perhaps the relevant differences are also related to the fact that adaptation to laterally displacing prisms affects head-centered directions, whereas movements on a surface to control the position of the cursor on a monitor are controlled primarily in a frame of reference which is centered on the current start location of the movement (Heuer and Sangals 1998).

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