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Compensation for and adaptation to changes in the environment

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Abstract Human motor behavior is remarkably accurate, even though many everyday skills require flexible adjustments between motor activity and its consequences in extracorporeal space. The present study addressed two questions: first, how do people compensate for unpredictable changes in the environment, and second, how do they adapt to such changes? In Experiment 1, participants repeatedly and continuously drew up and down strokes on a writing pad. After drawing under a base mapping, either (a) a change of target position, or (b) a change of gain, or (c) both occurred. Compensation for gain changes occurred later than compensation for changes in target position. In addition, there were aftereffects of the previous movement in accuracy and movement time. Adaptation to changes occurred in reference to extracorporeal space, with motor constraints as a limiting factor. In Experiment 2 we obtained similar effects when participants had more time to adapt. The view that movements are planned in reference to their goals in extracorporeal space is supported.

Keywords Compensation · Adaptation · Tool transformation · Extracorporeal space

Introduction

Human motor behavior is remarkably accurate, even though many aspects of the environment change over time. Accordingly, many everyday skills require that

people flexibly adjust their movements to some type of transformation between motor activity and its consequences in extracorporeal space. Imagine for instance drilling a hole into the wall. The stonework consists of different layers differing in density. With every new layer, the person holding the drill needs to adjust pressure to the new density. She or he will initially compensate for the sudden change and later adapt to it.

The present study addresses the two issues of how one compensates for unpredictable changes in the environment and how one adapts to them. The changes we investigate are changes in action-effect transformations and changes of target positions. To this end, we used a drawing task that required continuous and repetitive movements to be performed. Before we go into the details of the present study we will briefly address relevant prior research.

A popular idea is that the CNS controls movements using internal models (Wolpert and Flanagan 2001). According to the internal model approach, when we perform a movement, a forward model predicts the sensory consequences of each motor command. The predictions can refer to bodily consequences (such as how our arm moves) but are not restricted to them. For instance, predictions about the movement of a tool (for example a hammer) can also be generated (Wolpert and Flanagan 2001). When we direct our behavior towards objects in the environment that exhibit stable properties such predictive control mechanisms can be effectively exploited. However, our environment is often less predictable. For instance, in the above-mentioned example, the density differences of the stonework are not predictable for the person holding the drill. In such unpredictable situations movements are modified in response to sensory feedback, with the consequence that adjustment lags behind (Wolpert and Flanagan 2001). Therefore, compensation for unpredictable changes is usually not immediately perfect. When sudden changes in environmental conditions occur, the movement is usually started with the previously-used internal model, which is then modified during the movement. Thus,

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aftereffects of the previous movement, reflecting specifications of the pre-programmed movement (Dancause et al. 2002; Fukushi and Ashe 2003; Shadmehr and Mussa-Ivaldi 1994), do occur.

The CNS is particularly sensitive to the occurrence of unexpected events or the absence of expected events. There are at least two qualitatively different types of changes in the environment that require corrections of ongoing movements. One is a change of the target position a movement is directed at. For example, when playing handball, one might prepare to throw the ball to a certain player, but suddenly realizes that another player is in a strategically better position. The movement needs to be altered accordingly. A second possibility is that the relation between a movement and its consequences changes (the gain of the movement varies, Knoblich and Kircher 2004). For example when depressing the gas pedal in a car, the corresponding effects on speed vary depending on the gear one is currently using. Our study addresses both types of changes.

Forward models are not fixed entities, but they can be modified, trained, or updated through experience. The differences between the predicted and actual outcome of a motor command provide important information that can be used to adjust forward models (Wolpert and Flanagan 2001). This has, for example, been shown in studies with altered visual feedback (Prablanc et al. 1975). Many perturbation studies have also shown that people are able to adapt to changes in the visuomotor map such as the ones that occur when wearing prism glasses (Welch 1986) or as a result of other visual perturbations (Imamizu et al. 1995; Wolpert et al. 1995; Ghahramani et al. 1996; Kagerer et al. 1997). Some of these transformations are easier to adapt to than others. Depending on the type of transformation, it can take hundreds of trials before normal movement trajectories are regained (Imamizu et al. 1995; Shadmehr and Mussa-Ivaldi 1994), or only one or two trials (Fukushi and Ashe 2003; Dancause et al. 2002).

When people adjust to some type of transformation between motor activity and its visual consequences, it is the task of the CNS to estimate the current context (Vetter and Wolpert 2000). Current context refers to the properties of objects in the world and the prevailing environmental conditions. The estimation of current context is necessary to make movement planning with regard to the desired goal possible. It seems that flexible mappings between movements and their consequences in the external world are especially important for tool use.

One critical question in this context is, what is actually controlled by the CNS, or put differently, what are the organizing principles behind movement specification? Most researchers have focused on solving the problem of the inverse kinematics and inverse dynamics relation between end-point, joint angles and joint torques (Saltzman 1979; Soechting and Lacquaniti 1983). However, there is increasing evidence that movement

organization cannot be understood without taking the goals and effects of a movement in extracorporeal space into account (Mechsner et al. 2001). For example, Flash and Hogan (1985) have argued that simplicity of motor control is achieved by planning hand trajectories in (extracorporeal) space. Joint rotations are then tailored to produce these desired hand movements. This view has gained support by studies showing that movement kinematics show many invariant features, regardless of where in space they are performed. For example, when moving one of the hands to a target, participants tend to generate roughly straight trajectories (Abend et al. 1982; Morasso 1981; Shadmehr and Mussa-Ivaldi 1994; Wolpert et al. 1995, but also see Atkeson and Hollerbach 1985; Desmurget et al. 1997 for differing results in vertical and unconstrained movements, respectively). These results strongly suggest that planning takes place in terms of hand trajectories rather than joint rotations (Flash and Hogan 1985; Flash and Henis 1991; Soechting and Flanders 1989).

However, most of these studies used hand position as visual feedback, and thus it is difficult to distinguish whether movement planning occurs in terms of hand kinematics, or in terms of extracorporeal kinematics of the movement in perceived space. The necessity to distinguish between these two possibilities becomes obvious when one considers the above-mentioned examples of tool-use. Holding or using a tool like a pen or a hammer implies that there is a specific relationship (transformation) between the movement of the hand and the consequences in extracorporeal space. Studies using artificial visual feedback suggest that it is indeed the extracorporeal space in which hand movements are planned. The importance of the extracorporeal visual reference frame has been demonstrated for discrete unimanual (Flanagan and Rao 1995; Rogosky and Rosenbaum 2000; Rosenbaum and Gregory 2002; Wolpert et al. 1995) as well as bimanual coordinative movements (Mechsner et al. 2001).

One theoretical approach that focuses on the relationship between movements and their intended consequences is the ideomotor approach to voluntary action (Greenwald 1970; James 1890). A recent version of this approach, the common coding theory, assumes that performing voluntary actions involves a level of representations that code distal events (Hommel et al. 2001; Prinz 1992, 1997). This implies that movement production is guided by codes that specify the goals certain actions should have in extracorporeal space.

Experiment 1

The present experiment deals with compensation for and adaptation to unpredictable changes in the environment, as outlined above. In contrast to many previous studies, we (1) investigated compensation and adaptation to changes in a continuous task (see however Pellizer et al. 1999; Tong and Flanagan 2003 for studies using con-

tinuous tasks), (2) addressed reduction and extension of the amplitude instead of the sideward displacement of the target, and (3) addressed changes of target position and gain changes in the same experiment. We chose continuous, repetitive movements (more specifically, drawing up and down strokes) in order to be able to capture modifications of internal models for both target and gain changes. In the present drawing task, immediate compensation can be addressed by analyzing the kinematics of the first stroke that follows a certain change. Adaptation can be addressed by analyzing the kinematics of strokes that are performed some time after the onset of the change.

We expected that the compensation for gain changes has a later onset than the compensation for target changes. In the former case participants need to detect a discrepancy between an internally predicted and an observed location on the screen; this information needs to be accumulated. In contrast, target changes can be directly perceived. In addition, we expected aftereffects of the previous movement, that is, overshoot when a reduction of movement amplitude was required, and undershoot when an extension was required. We expected these effects to be more pronounced in response to gain changes than in response to target changes, because of the hypothesized differences in compensation onset.

We also included a condition that required a change of the visuomotor-map without any alteration in the movement to be performed. In this condition the gain change neutralized the target change. Thus, we expected that participants first realize that a change in target position has taken place, and that they then try to alter their movement accordingly. Only later do they notice that there was an additional gain change and therefore start to compensate in the opposite direction. Any performance differences in comparison to the baseline reflect attempts of unnecessary compensation. In terms of accuracy, we expected to see an over- or undershoot of the movement in the direction of the first compensation.

Regarding adaptation, we assumed that participants would adapt relatively quickly, because it should be relatively easy to extend and reduce movements in response to extension and reduction transformations. Our main goal was to determine whether vision (extracorporeal space) affects the organization of the adapted movement. In accordance with the ideomotor principle we assumed that movements of the same amplitude would be performed differently depending on the visual context. To address this issue, we compared the kinematic parameters for conditions that required the same movement but differed in visual context (visual amplitude, gain). If movement parameters do not differ between those conditions, then visual context does not affect the specification of movement kinematics. If movement parameters differ in a systematic way between those conditions, the visual reference frame in extracorporeal space plays an important role for movement organization.

Method

Participants

Ten students (six female) from Munich universities took part in the experiment. All participants were right-handed. Mean age was 22.5 (SD = 2.7) years. Participants were paid 24 German Marks for participation in the experiment. The local ethics committee approved the study.

Materials and apparatus

Stimuli were presented on a 17" screen, with a resolution of 600×800 pixels. The vertical screen refresh rate was 75 Hz. Movements were recorded with a Wacom Ultrapad A3 writing pad at a resolution of 500 pixels per cm and at a rate of 100 Hz.

The screen displayed two horizontal lines. Participants performed up and down strokes between these lines. One line remained in a fixed position throughout the experiment; the other shifted in position due to experimental conditions (see below). There were two sessions. In one session the lower line remained fixed, in the other session the upper line remained fixed. The order of sessions was counterbalanced across participants.

In the following, the layout with the upper line in a fixed position is described as an example. The fixed line was presented 6 cm below the top of the screen and had a horizontal length of 3 cm. In the baseline condition, the lower line was presented at 8 cm below the upper line. This distance of 8 cm on the screen corresponded to 10 cm on the writing pad. Our description of the experimental conditions will be made in reference to this distance, which will be called the "base unit".

Three types of manipulations were introduced relative to the baseline: (a) a change of target position, (b) a change of gain between movement amplitude and visual amplitude, and (c) a simultaneous change of target position and change of gain (target + gain). For each manipulation there were two levels of reduction (small and large) of either movement amplitude and/or visual amplitude (relative to the baseline), and two levels of extension (small and large). Table 1 depicts the visual amplitude, movement amplitude, and the corresponding gain for each cell in the design. Figure 1 illustrates the experimental conditions.

Procedure

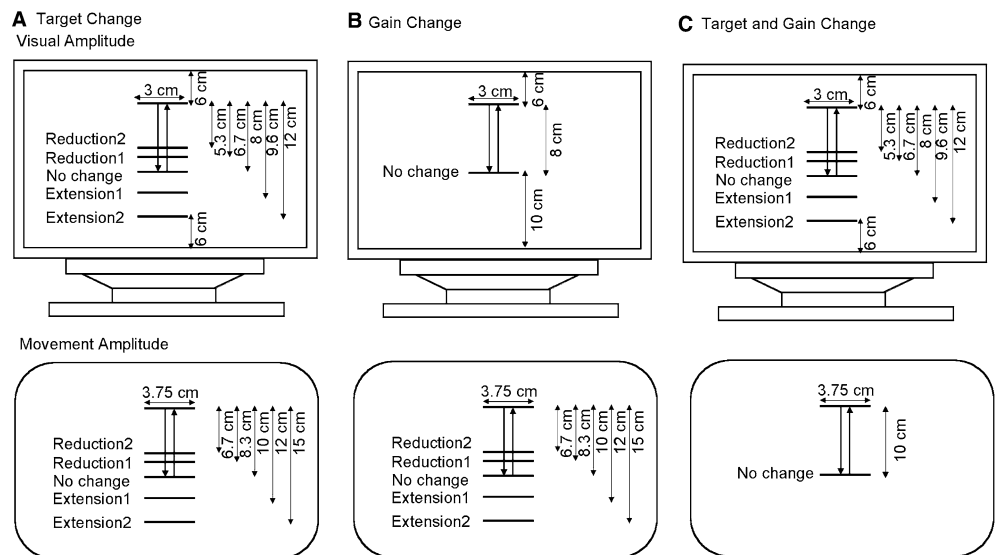
The experiment took place in a dimly lit room. The writing pad was placed in front of the participants at a height that allowed for comfortable drawing. A cover screened the hands from view. The monitor was posi-

Table 1 Experimental conditions for Experiment 1

	Reduction 2	Reduction 1	Extension 1	Extension 2
Change of target position				
Movement amplitude	0.6667	0.8333	1.2	1.5
Effect amplitude	0.6667	0.8333	1.2	1.5
Gain	1	1	1	1
Change of gain (same effect)				
Movement amplitude	0.6667	0.8333	1.2	1.5
Effect amplitude	1	1	1	1
Gain	1.5	1.2	0.8333	0.6667
Change of target position and gain (same movement)				
Movement amplitude	1	1	1	1
Effect amplitude	0.6667	0.8333	1.2	1.5
Gain	0.6667	0.8333	1.2	1.5

Movement amplitudes and effect amplitudes are depicted in base units. Base units refer to the no change condition. Thus the values in the table represent a relative to this condition. 1 equals 10 cm on the writing pad and 8 cm on the screen

Fig. 1A–C Illustration of the experimental conditions relative to the baseline for Experiment 1. **A** Change of target position: the target position is presented at either a reduced or an extended amplitude (two levels each), and the movement needs to be reduced or extended correspondingly. **B** Change of gain: the visual amplitude remains the same, but the movement needs to be reduced or extended. **C** Target and gain change: the visual amplitude changes, but the required movement amplitude remains the same. The drawing is not to scale; however, distances are given



tioned behind the writing pad, at a slightly higher level. Participants were seated 60 cm away from the monitor.

Participants were instructed to continuously draw straight strokes between the two lines displayed on the screen. As soon as they reached a line, they were to reverse the direction without pausing on the line. The instruction stressed the need to move continuously and to turn accurately. Participants needed to control their movements exclusively on the basis of the visual information about target and cursor position, because they could not see their hands. At the start of each trial a red box (0.5×0.5 cm) appeared at the starting position directly above and centered on the top line. The trial started as soon as participants entered the box. After that, participants drew three down strokes and three up strokes under the base mapping (baseline: strokes 1–6). Then, one of the experimental conditions set in. This condition lasted again for six strokes (three down and three up: strokes 7–12). Afterwards, six strokes were drawn under the base mapping (strokes 13–18). Then another experimental condition set in for the following

six strokes (19–24), and so on. After each experimental condition the baseline condition re-established the base mapping. The baseline condition was also repeated as one experimental condition. Each trial thus consisted of 81 upstrokes and 81 downstrokes (13 experimental conditions, 14 base mappings, each with three up and three down strokes). The order of the different experimental conditions was randomized within each trial. Participants performed 42 trials, 21 starting at the bottom and 21 starting at the top. The first trial was always excluded from the analyses.

Data preparation

Only the *y*-axis was analyzed because participants only made vertical movements. Deviation along the *x*-axis (horizontal dimension) within strokes was small (1–3 mm) and did not differ significantly between conditions. In a first step, we interpolated the position data to yield a constant sample rate of 100 Hz because there was

some variation in the sampling rate of the writing pad (7–13 ms). In a second step, the kinematic data were smoothed using an algorithm proposed by Mottet et al. (1994). In a third step, pen velocity was determined at each point in time. Stroke onset was defined as the point in time and space when participants were at the reversal points of the movements. In case participants did not move continuously, the respective strokes were excluded from further analyses. The criterion was that a participant did not move more than 1 mm within the first 50 ms after the begin of a stroke. In addition, strokes shorter than 200 ms were excluded from further analyses, because it is unlikely that participants had time to correct movements with respect to the changes introduced. 12.5% of the strokes were excluded using these criteria.

Data analysis

To characterize the way participants compensated for the changes, we analyzed accuracy, movement time, and compensation onset for the stroke immediately following the introduced change. Any kinematic characteristics that differed from the baseline (no change) condition were regarded as compensatory. Accuracy was defined as the deviation from the position of the target line (in mm). Negative values indicate undershoots, positive values indicate overshoots. Movement time for each stroke was calculated as the time between movement onset and movement reversal (in ms). Compensation onset was determined in the following way. In the target change and the gain change condition, compensation onset was calculated by comparing the position data with the no change condition. For the target + gain change conditions, calculation of compensation onset relative to the no change condition yields the time when both changes are compensated for. Therefore, to calculate onset of target change compensation we compared the position data in the target + gain change condition with the position data in the gain change condition. To calculate onset of gain change compensation, we compared the position data in the target + gain change condition with the position data in the target change condition.

We used a method adapted from Brenner and Smeets (1997) to determine the compensation onset. One-tailed Mann–Whitney *U*-tests were calculated for each point on the position curves of two conditions of stroke 1. The first point at which the trajectories differed significantly and which was followed by at least four more points at which the trajectories also significantly differed was defined as the compensation onset. This analysis was repeated for all comparisons between curves and performed for each participant separately. The resulting values are actually a slight overestimation of compensation onset, because the changes due to a new condition were only introduced after two data samples consistently indicated that participants had reversed the direction of

movement. Given the refresh rate of 75 Hz, this means that the first alterations on the screen occurred between 20 ms and 33.3 ms after the onset of a new stroke. Thus, compensation time is overestimated by 26.6 ms, in average. The values reported in the following were corrected using this estimation.

To characterize adaptation, we calculated accuracy and movement time (naturally, compensation onset cannot be computed for later strokes); in addition, we analyzed peak velocity. This was calculated as the maximal velocity occurring during each stroke (in mm/s).

Results

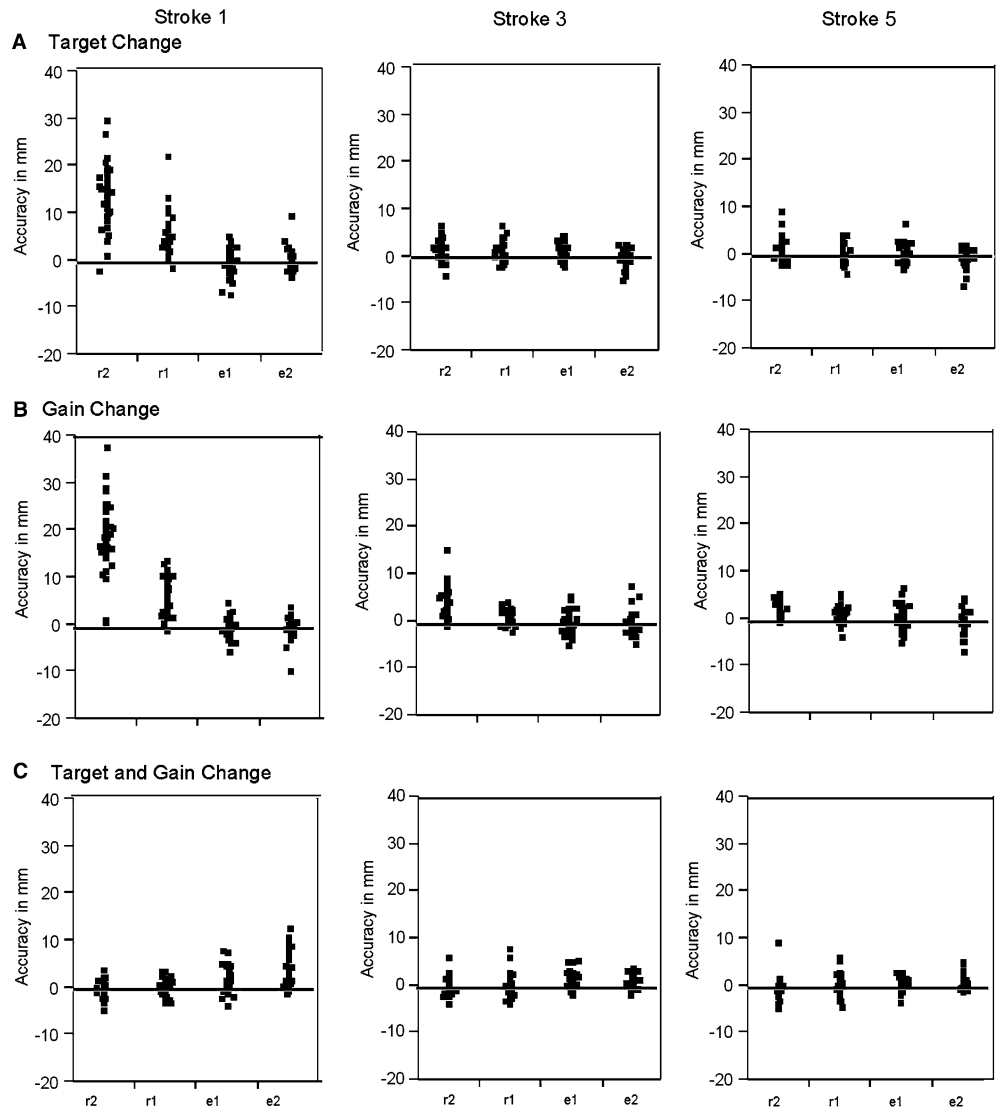
Because there were no differences in performance depending on whether participants started at the bottom or at the top of the screen we collapsed the data across these conditions. In the following, we will only report the results for the first and fifth stroke performed after an experimental condition. An initial inspection of the kinematic data showed that the second, fourth and sixth strokes did not yield any further information about the way participants compensated or adapted, but rather reflected a “going back to the starting position” (so that smaller effects of the introduced changes on accuracy were found). The results for the third stroke are also not reported, because the pattern of results largely resembled the ones for stroke 5. However, to illustrate behavior across the adaptation process, Fig. 2 shows accuracy data from one participant for strokes 1, 3, and 5 for all conditions in which a change occurred as an example.

Data were analyzed with two separate ANOVAs for each dependent variable, apart from the analysis of compensation onset (CO). The target change and the gain change condition were analyzed in one ANOVA. This is adequate because the corresponding reduction and extension levels required the same movement. The target + gain change condition and the no change condition were analyzed in the second ANOVA; here the same movement is required on all levels. *T*-tests were used to further assess differences between levels.

Compensation (stroke 1)

For stroke 1 we analyzed compensation onset (CO), accuracy (AC) and movement time (MT). We start with CO to test our assumption that target changes are detected earlier than gain changes. The predictions for AC and MT differ depending on CO and are therefore reported in the second step. The mean velocity profiles over participants are illustrated in Fig. 3. Panels A, B, and C show the mean velocity profiles for the different conditions and illustrate how participants compensated for the various changes; the exact values for CO can be

Fig. 2A–C Endpoint accuracy for strokes 1, 3, and 5 in Experiment 1: **A** for the target change condition; **B** for the gain change condition, and; **C** for the target and gain change condition. *r2*, reduction 2; *r1*, reduction 1; *e1*, extension 1; *e2*, extension 2. Negative values reflect undershoot, positive values reflect overshoot of the movement. The *line* represents performance in the baseline condition



found in Table 2. Results for MT and AC of stroke 1 can be found in Table 3.

Compensation onset (CO)

To compare the compensation onset in all conditions, a repeated measurements ANOVA with the factors condition (single change, combined change), type of change (target change, gain change), direction of change (reduction, extension), and extent of change (small, large) was conducted on CO. There was a significant effect for type of change ($F_{(1,9)}=62.3$, $P<0.001$), indicating that the CO occurred later in the gain change (403 ms) than in the target change (318 ms) condition. In addition, there was a significant effect for direction of change ($F_{(1,9)}=7.0$, $P=0.03$), indicating that a reduction (351 ms) lead to faster compensation than an extension (371 ms). We also obtained a tendency for extent of change ($F_{(1,9)}=3.2$, $P=0.1$), which reflects a tendency for large changes (354 ms) to evoke faster compensation

than small changes (368 ms). The effect of condition and all interactions were not significant.

Thus, our hypothesis that the onset of the compensation for gain changes would occur later than the one for target changes was verified. Furthermore, there was some indication that compensation for large changes had an earlier onset than compensation for small changes. In addition, reductions of visual and/or movement amplitude lead to faster compensation than extensions of the amplitudes.

Accuracy (AC)

A repeated-measurements ANOVA with the factors type of change (target change, gain change) and movement amplitude (reduction 2, reduction 1, extension 1, extension 2) revealed a significant main effect for type of change ($F_{(1,9)}=87.3$, $P<0.001$), a significant main effect of movement amplitude ($F_{(3,27)}=125.9$, $P<0.001$), and a significant interaction between these factors

Fig. 3A–F Mean velocity profiles averaged across all participants in Experiment 1. **A–C** Compensation (stroke 1). **D–F** Adaptation (stroke 5).

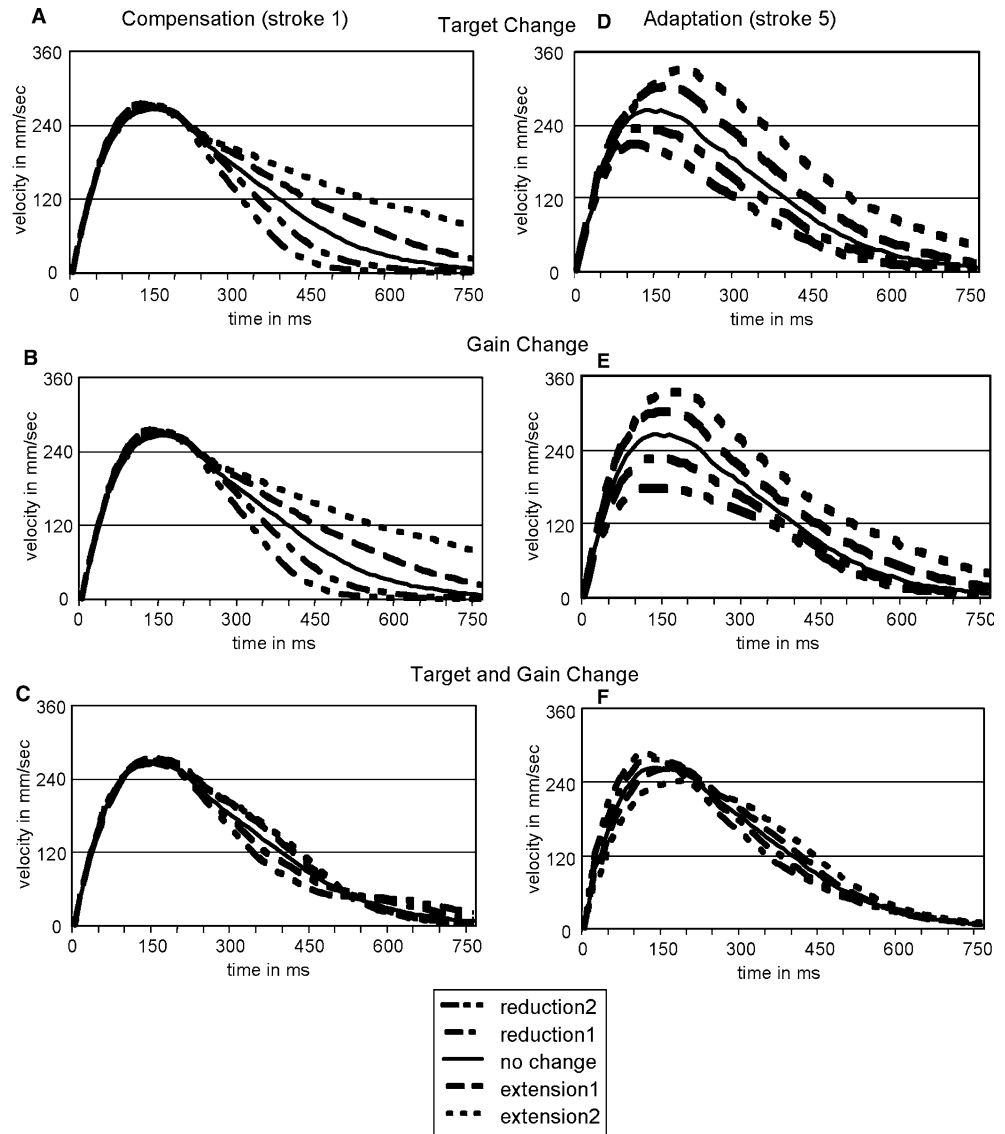


Table 2 Compensation onset in stroke 1 in Experiment 1

Time taken to react to change of target position (in ms)				Time taken to react to gain change (in ms)			
Reduction 2	Reduction 1	Extension 1	Extension 2	Reduction 2	Reduction 1	Extension 1	Extension 2
Condition: change of target position							
312 (39)	333 (80)	327 (43)	327 (26)				
Condition: change of gain							
				370 (22)	408 (29)	423 (32)	412 (33)
Condition: change of target position and change of gain							
308 (95)	274 (93)	340 (49)	320 (116)	385 (38)	412 (33)	422 (55)	393 (72)

($F_{(3,27)} = 37.3$, $P < 0.001$). This pattern of results reflects that there was significant undershoot when the movement amplitude was extended and significant overshoot when it was reduced. These effects were more pronounced in the gain change than in the target change condition (range from 17.9 mm to -2.7 mm versus range from 12.4 mm to -1.3 mm), consistent with later CO in the gain change condition.

A separate repeated-measurements ANOVA on AC with the factor visual amplitude (reduction 2, reduction 1, no change, extension 1, extension 2) was computed for the target + gain change condition. It revealed a significant main effect for visual amplitude ($F_{(4,36)} = 37.6$, $P < 0.001$). Post hoc comparisons revealed that all visual amplitude levels were different from the no change condition (all $P < 0.005$). Reduction of the visual

Table 3 Movement time (in ms) and accuracy of movement (in mm) of stroke 1 in Experiment 1

	Reduction 2 M (SD)	Reduction 1 M (SD)	Extension 1 M (SD)	Extension 2 M (SD)
Accuracy of movement (mm) ^a				
Target change	12.4 (4.7)	4.0 (2.5)	-1.3 (2.0)	-1.3 (2.7)
Gain change	17.9 (3.8)	6.7 (2.6)	-1.0 (1.6)	-2.7 (2.2)
Target and gain change	-1.8 (1.8)	-0.5 (1.1)	1.6 (1.8)	3.6 (2.8)
No change		0.1 (1.0)		
Movement time (ms)				
Target change	437 (36)	529 (58)	799 (93)	1036 (115)
Gain change	443 (27)	515 (41)	842 (89)	1080 (132)
Target and gain change	760 (139)	706 (95)	606 (54)	618 (54)
No change		650 (78)		

^aA positive value indicates an overshoot of the target line, a negative value an undershoot

amplitude resulted in undershoot and extension of visual amplitude resulted in overshoot, reflecting errors in the direction of the first compensation.

Movement time (MT)

To compare the target change and gain change conditions, a repeated-measurements ANOVA was computed on MT with the factors type of change (target change, gain change) and movement amplitude (reduction 2, reduction 1, extension 1, extension 2). It revealed a significant main effect for type of change ($F_{(1,9)}=23.0$, $P=0.001$), a significant main effect for movement amplitude ($F_{(3,27)}=292.2$, $P<0.001$), reflecting an increase in MT with movement amplitude, and a significant interaction of type of change \times movement amplitude ($F_{(3,27)}=4.7$, $P=0.009$). MTs in the gain change condition were longer than in the target change condition for the extended movements (all $P<0.05$), but not for the reduced movements, which again is consistent with later CO in the gain change condition.

A separate ANOVA on MT for the target+gain change condition with the factor visual amplitude (reduction 2, reduction 1, no change, extension 1, extension 2) revealed a significant main effect for visual

amplitude ($F_{(4,36)}=19.7$, $P<0.001$). MTs were generally longer when visual amplitude was reduced compared to the no change condition (both $P<0.005$). A small extension in visual amplitude reduced MT ($P=0.001$); for the large extension there was a trend in the same direction ($P=0.07$). This is consistent with the assumption that participants initially (unnecessarily) compensate for the target change and then compensate for the gain change, trying to counteract the first compensation.

Adaptation (stroke 5)

Obviously CO cannot be calculated for stroke 5, because movements have already been adapted to the new environment and the stroke kinematics are different right from the start. Instead, peak velocity (PV) is analyzed to characterize movement kinematics in addition to MT. Mean velocity profiles for the participants can be seen on the right side of Fig. 3 (D–F) and give an impression of how participants adapted to the introduced changes. Table 4 gives the exact values of AC, MT, and PV.

The rationale behind the following analysis was as follows: If movements of the same amplitude differ

Table 4 Movement time (in ms), accuracy of movement (in mm), and peak velocity of movement (in mm/s) of stroke 5 in Experiment 1

	Reduction 2 M (SD)	Reduction 1 M (SD)	Extension 1 M (SD)	Extension 2 M (SD)
Accuracy of movement (mm) ^a				
Target change	1.3 (1.6)	0.5 (1.1)	-0.2 (1.3)	-0.8 (0.9)
Gain change	2.5 (1.6)	1.0 (1.5)	-0.6 (1.8)	-1.8 (2.1)
Target and gain change	-1.0 (1.7)	-0.3 (1.3)	0.5 (1.2)	0.8 (1.6)
No change		0.1(1.1)		
Movement time (ms)				
Target change	571 (83)	610 (72)	732 (99)	903 (93)
Gain change	587 (66)	622 (71)	737 (78)	825 (91)
Target and gain change	626 (101)	636 (89)	663 (74)	701 (73)
No change		655 (99)		
Peak velocity of movement (mm/s)				
Target change	253 (28)	284 (30)	382 (52)	406 (46)
Gain change	238 (27)	280 (27)	373 (42)	408 (46)
Target and gain change	348 (47)	341 (36)	323 (30)	315 (28)
No change		332 (41)		

^aA positive value indicates an overshoot of the target line, a negative value an undershoot

systematically in their kinematics (MT, PV) under different visual conditions, this effect can be attributed to the role of vision, that is, extracorporeal space in movement control. If movement parameters are optimized regardless of visual context, they should be the same for movements of the same amplitude.

As in the previous analyses, we compared the target change with the gain change condition, because they require the same movements on each level. We expected that a main effect of movement amplitude would be obtained in this analysis. If movement amplitude is sufficient to specify movement parameters, there should be no main effect of type of change and no interaction between type of change and movement amplitude. If any of those effects occur this would indicate that movement amplitude is not sufficient to specify the movement and that vision does have an effect. The target+gain change condition was again analyzed in a separate ANOVA (including the no change condition). All of the levels required the same movements, but differed in visual amplitude. Thus, if movement amplitude is sufficient to specify the movement, there should be no effect of visual amplitude. On the other hand, if a significant effect for visual amplitude is obtained, it can be concluded that visual amplitude has an influence on movement specification. For this analysis the effect size (partial η^2) is also reported, because it indicates the impact vision has on the specific parameters. To exclude the possibility that observed effects can be accounted for by Fitts' law, we also analyzed the data according to Fitts' law (for details see below).

Accuracy (AC)

AC was relatively high in the fifth stroke (range: from -1.8 mm to 2.5 mm), which shows that participants had adapted fairly well to the condition by the fifth stroke. However, adaptation was not perfect; although the effects were small in size, there were systematic variations corresponding to the pattern observed for stroke 1 (the range of deviation in stroke 1 was from -2.7 mm to 17.9 mm).

A repeated-measurements ANOVA on AC with the factors type of change (target change, gain change) and movement amplitude (reduction 2, reduction 1, extension 1, extension 2) revealed no significant effect for type of change ($F_{(1,9)}=0.41$, $P=0.84$), a significant main effect of movement amplitude ($F_{(3,27)}=59.2$, $P<0.001$), and a significant interaction between these two factors ($F_{(3,27)}=14.0$, $P<0.001$). The target change and gain change condition differed only in the large reduction and extension levels (reduction 2 and extension 2, both $P<0.05$). The reduced movement showed more overshoot in the gain change (difference: 1.2 mm) than in the target change (difference: 1 mm) condition. The extended movement showed more undershoot in the gain than in the target change condition.

For the target+gain change condition a repeated-measurements ANOVA on AC was conducted with visual amplitude (reduction 2, reduction 1, no change, extension 1, extension 2) as the independent factor. It revealed a significant main effect for visual amplitude ($F_{(4,36)}=18.4$, $P<0.001$). Post hoc comparisons revealed that all but one visual amplitude level were different from the no change condition, the reduction 1 level (small reduction) showed only a tendency (all $P<0.07$). Reduced visual amplitudes resulted in overshoot and extended visual amplitudes resulted in undershoot.

Due to the gain change in some conditions it might be that AC differences in movement coordinates might in fact not be present in visual coordinates. This was, however, not the case. The same pattern of results was still obtained when data were transformed to visual accuracy coordinates.

Movement time (MT)

An ANOVA on MT with type of change (target change, gain change) and movement amplitude (reduction 2, reduction 1, extension 1, extension 2) revealed no significant effect for type of change ($F_{(1,9)}=2.2$, $P=0.18$) and a significant main effect of movement amplitude ($F_{(3,27)}=101.0$, $P<0.001$). This effect demonstrates that MT depends on movement amplitude. There was also a significant interaction between type of change and movement amplitude ($F_{(3,27)}=14.8$, $P<0.001$). As indicated by the interaction, the range of MTs was lower in the gain change condition (same visual amplitude, 238 ms) than in the target change condition (different visual amplitudes, 332 ms, $P<0.001$).

An ANOVA on MT in the target+gain change condition with visual amplitude (reduction 2, reduction 1, no change, extension 1, extension 2) as an independent factor revealed a significant main effect for visual amplitude ($F_{(4,36)}=10.5$, $P<0.001$). Partial η^2 was 0.54 . Comparisons revealed that MTs were shorter in the reduced visual amplitudes in comparison to the no change condition. In addition MT was longer with the large extension of visual amplitude (all $P<0.05$). (Note also that those effects are opposite to the MTs in the compensation strokes.)

Thus, the results of both ANOVAs suggest that visual context does play a role in the determination of movement kinematics.

Peak velocity (PV)

A repeated-measurements ANOVA on PV with the factors type of change (target change, gain change) and movement amplitude (reduction 2, reduction 1, extension 1, extension 2) revealed a significant effect for type of change ($F_{(1,9)}=5.9$, $P=0.04$), indicating that peak velocity was higher in the target change condition than

in the gain change condition. The significant main effect of movement amplitude ($F_{(3,27)}=119.5$, $P<0.001$) indicates that the larger the movement amplitude, the higher the peak velocity. There was no significant interaction type of change \times movement amplitude ($P_{(3,27)}=2.2$, $P=0.11$). However, when comparing levels separately, PV was only significantly higher for large reduction in the target change condition. This is consistent with the assumption that a higher gain should result in a lower PV.

A repeated-measurement ANOVA on PV in the target+gain change condition with the factor visual amplitude (reduction 2, reduction 1, no change, extension 1, extension 2) revealed a significant main effect for visual amplitude ($F_{(4,36)}=10.8$, $P<0.001$). Partial η^2 was 0.55. Comparisons revealed that reduced visual amplitudes (low gain) resulted in a significantly higher PV and large extensions (high gain) resulted in a significantly lower PV than in the no change condition (all $P<0.04$). This is again consistent with the assumption that visual context has an influence on movement kinematics.

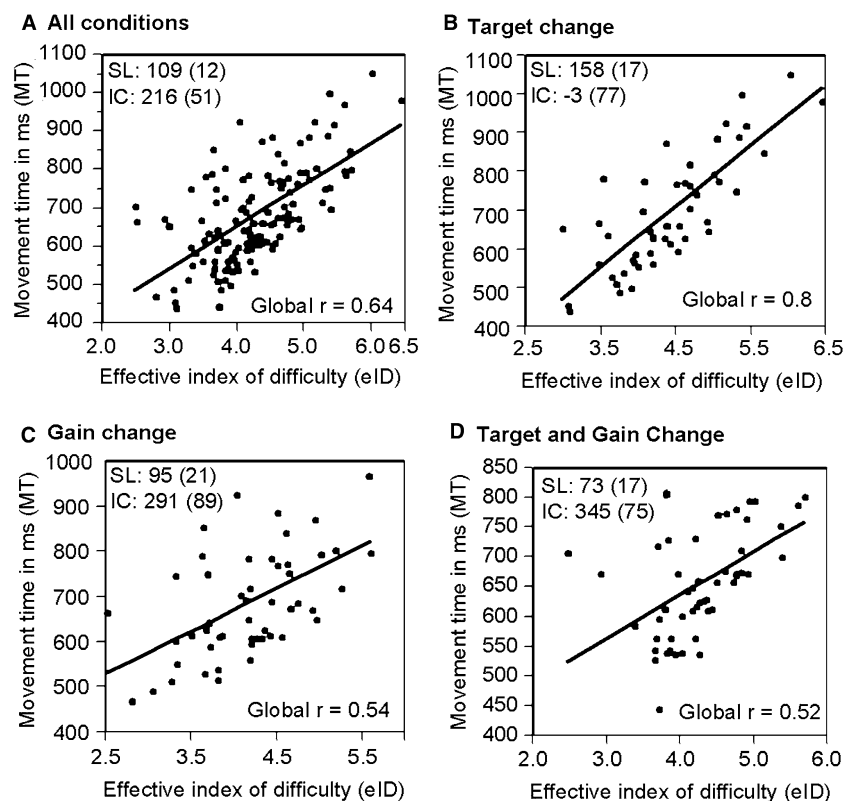
Adaptation and Fitts' law

Fitts' law (Fitts 1954) states that there is a linear relationship between movement time and movement difficulty (index of difficulty). On the one hand, one could be concerned that our task emphasized speed to

a lower degree than is usual in Fitts' tasks, which might change the task constraints and diminish the prediction power of the model (Meyer et al. 1988). On the other hand, however, one could also argue that the results we obtained in the adaptation phase can be explained by Fitts' law and do not really reflect movement organization according to external space. For example, in the target+gain change condition, in spite of equal movement amplitudes, target width differs due to the gain changes. Thus, it could be that the obtained differences in movement time are due to variation in the index of difficulty. To investigate this issue we calculated the effective index of difficulty (eID), using effective target width (Welford 1968, pp 147–148) for stroke 5 in all conditions. We computed correlations with eID and MT. The individual correlations were z -transformed (Fisher's z -transform) for each condition and each participant. T -tests were run on those transformed values. The average correlations reported here in the text are reconverted from the average Fisher's z -values. As an illustration, Fig. 4 shows global fittings (over the individual data points from all participants) of Fitts' functions, which complement the correlation analysis. Note that the correlations reported in the figure are slightly different than those used for statistical analysis: in the figure the correlations are calculated globally over participants and condition levels.

The overall correlation for all conditions was $r=0.53$. This correlation of eID and MT seems to be smaller

Fig. 4A–D Global fittings of the data of stroke 5 according to Fitts' law for Experiment 1. The individual data points of the participants are presented. **A** All conditions, **B** target change, **C** gain change, **D** target and gain change. The baseline is always included in the fit. r , correlation between effective index of difficulty (eID) and movement time (MT); SL , slope of the function; IC , intercept of the function. Standard errors for SL and IC are in parentheses



than the correlations generally reported in the literature (for instance, $r=0.79$ in Fitts and Peterson 1964). To investigate whether the low correlation for eID and MT was due to different strengths of association in the three change conditions, we calculated the correlation of eID and MT separately for the three types of changes (always including the baseline no change condition). The correlation eID and MT was high within the target change condition ($r=0.84$). In the gain change condition ($r=0.45$) and in the target+gain change condition ($r=0.46$) the correlations were significantly lower than in the target change condition ($t(9)=2.4$, $P=0.04$; $t(9)=2.74$, $P=0.02$, respectively). The gain change and target+gain change conditions did not differ significantly from each other ($t(9)=0.05$, $P=0.96$). As Fig. 4 illustrates, the fitting functions also seem to differ between the three types of change condition. The pattern of correlation is similar to the one reported here. Thus, Fitts' law seems to be able to explain behavior fairly well in conditions where only amplitudes differ; however, it does not account well for conditions in which gains differ.

Discussion

In the present experiment we investigated (1) the compensation for, and (2) the adaptation to suddenly introduced changes of target position and/or gain in a task that required continuous drawing of up and down strokes. As predicted, compensation for gain changes had a later onset than compensation for target changes. Furthermore, changes implying reduction were compensated for earlier than changes implying extension, and there was a tendency for compensation to occur earlier when the changes were more drastic. We also observed the predicted aftereffects of the previous movement when changes were introduced. Shorter movements resulted in overshoots and longer movements in undershoots. This effect was more pronounced in the gain change than in the target change condition, which is consistent with the observation that participants compensated later in the former condition. In accordance with the results for the compensation onset, larger movement amplitudes resulted in higher movement times in the gain change condition in comparison to the target change condition. In the target+gain change condition, we predicted (unnecessary) attempts to compensate. Accordingly, there was undershooting when the visual amplitude was reduced, and overshooting when the visual amplitude was extended. Consistent with this overcompensation, shorter visual amplitudes resulted in longer movement times, and longer visual amplitudes resulted in shorter movement times than in the no change condition.

The second goal of this experiment was to investigate how people adapt to the modified conditions (analysis of stroke 5). Specifically, we aimed to find out

whether movement parameters would differ when comparing conditions that require the same movements but have different visual characteristics. Stroke 5 was generally drawn quite accurately (ranging from -1.8 mm to 2.5 mm under- and overshoot). Movement times under the gain change condition were more homogeneous than under the target change condition—that is, short movements were slower and long movements were faster for the gain change as compared to the target change condition. Movement times in the target+gain change condition were positively related to visual amplitude. Both results indicate that visual context is important to the control of movement. In the analysis of peak velocity, comparison of the target change condition versus the gain change condition gave some indication of the role of vision, whereas analysis of the target+gain change condition was unequivocally in favor of the role of vision in determining peak velocity. Short visual amplitudes resulted in the highest peak velocities (coinciding with shorter movement times), presumably because the cursor moves more slowly on the screen, and visual control can thus be exerted with high movement speed, whereas long visual amplitudes require lower peak velocity for the movement, when controlled visually. Fitts' law did not seem to be able to account for those results.

Experiment 2

The data on adaptation in Experiment 1 provided evidence that the visual reference frame in extracorporeal space has an influence on movement parameters. Fitts' law did not seem to be able to explain the observed results. However, one might be concerned that adaptation was not complete in stroke 5, and that the results therefore reflect behavior before the CNS is in its optimal state. It is therefore still possible that participants behave according to Fitts' law when full adaptation is reached, regardless of the visual reference frame. To provide further evidence that these effects cannot be explained by incomplete adaptation or by Fitts' law we conducted another experiment, Experiment 2. This time we did not provide any sudden mapping changes within the task. Rather, there was only one gain condition within each trial so that participants were likely to be adapted to it after a certain time. Moreover, movement amplitude and movement target width (and therefore index of difficulty) were the same for all conditions. However, the mapping of movement space to visual space differed between conditions. According to Fitts' law, movement times should be the same under all conditions. Thus, any systematic differences in movement time between conditions must be attributed to the influence of the visual reference frame on movement organization.

Method

Participants

20 students (10 male, 10 female) from various Munich universities took part in the experiment. All participants were right-handed. Mean age was 23.9 (SD = 3.9) years. Participants were paid 8 Euros for participation in the experiment. The local ethics committee approved the study.

Materials and apparatus

Only differences to the previous experiment are described here. The screen displayed two boxes arranged symmetrically above and below the horizontal midline. Participants had to perform up and down strokes between these boxes. The boxes had horizontal lengths of 4 cm. The vertical sizes and positions of the boxes were fixed within a trial, but varied between trials/conditions. Furthermore, the gain between movement and visual display differed between conditions. The gain was chosen to equalize the conditions in terms of movement amplitude (12 cm) and movement target width (0.4 cm) in movement space. The index of difficulty was therefore fixed at 5.91. See Table 5 for movement amplitude, movement target width, visual amplitude, visual target width and the corresponding gain for the nine conditions conducted in the experiment.

Procedure

Participants were instructed to continuously draw up and down strokes between the two boxes displayed on the screen and to reverse direction on the boxes without pausing on them. At the start of each trial, a red box (0.5×0.5 cm) appeared at the starting position in the middle of the screen. The trial started as soon as participants entered the box. The participants then moved continuously for 60 s. When the trial ended, the next trial, with a different condition, was started by the experimenter. There were nine trials within a block.

Participants performed four blocks, each containing all conditions in random order.

Data preparation and data analysis

Data preparation was the same as in Experiment 1. The first block and the first 10 s within a trial were not included in the data analysis. Movement time (MT) and peak velocity (PV) were analyzed as dependent variables.

Results

Results can be seen in Table 5. Repeated-measurements ANOVAs with the factor gain (1.8, 1.6, 1.4, 1.2, 1.0, 0.8, 0.6, 0.4, 0.2) were computed on MT and PV. The ANOVA on MT revealed a significant main effect for gain ($F_{(8,152)} = 19.58$, $P < 0.0001$), indicating that MT decreased with decreasing gain. Correspondingly, the ANOVA on PV also revealed a significant main effect for gain ($F_{(8,152)} = 9.79$, $P < 0.0001$), indicating that PV increased with decreasing gain.

Discussion

Experiment 2 was conducted to rule out the possibility that the effects observed during adaptation in Experiment 1 were due to incomplete adaptation, and to provide further evidence that Fitts' law is not able to explain the observed effects. To this end we kept movement amplitude and movement target width (and therefore index of difficulty) constant for all conditions. The gain between movement space and visual space, and correspondingly visual amplitude and visual target width, varied between conditions. Further, within one 60 s trial participants performed only strokes under one mapping, allowing for full adaptation. Movement time and peak velocity differed systematically between the different gain conditions. As in Experiment 1, movements with higher gain were slower and had lower peak velocity than movements with lower gain. This result replicates and extends the results of Experiment 1. It indicates that extracorporeal space has an effect on movement kine-

Table 5 Description of conditions (visual movement amplitude and visual target width in cm, gain), movement time (in ms), and peak velocity (in mm/s) in Experiment 2

Amplitude is calculated from the centers of the boxes. Movement amplitude was 12 cm and movement target width was 0.4 cm in all conditions. Index of difficulty was therefore constant at 5.9

Visual amplitude (cm)	Visual target width (cm)	Gain	Movement time (ms) M (SD)	Peak velocity (mm/s) M (SD)
21.6	0.72	1.8	851 (194)	221 (58)
19.2	0.64	1.6	830 (194)	226 (60)
16.8	0.56	1.4	828 (189)	228 (63)
14.4	0.48	1.2	800 (177)	236 (68)
12.0	0.40	1.0	785 (165)	244 (61)
9.6	0.32	0.8	754 (164)	247 (62)
7.2	0.24	0.6	741 (166)	251 (68)
4.8	0.16	0.4	721 (178)	256 (77)
2.4	0.08	0.2	682 (181)	261 (72)

matics, even when participants have a relatively long time to adapt. Fitts' law does not capture those effects, because according to Fitts' law movement times are predicted to be the same for all conditions.

General discussion

In the present study we investigated (1) the compensation for, and (2) the adaptation to suddenly introduced changes of target position and/or gain (Experiment 1). We were further interested in (3) the influence of extracorporeal space on movement kinematics after a relatively long time of adaptation (Experiment 2).

Concerning compensation in Experiment 1, gain changes were compensated for later than target changes, changes implying reduction were compensated for earlier than changes implying extension, and there was a tendency for compensation to occur earlier when the changes were more drastic. We also observed aftereffects of the previous movement when changes were introduced. Shorter movements resulted in overshoots and longer movements in undershoots. In the target + gain change condition we observed (unnecessary) attempts to compensate for the target change.

The second goal of Experiment 1 was to investigate how people adapt to the modified conditions (analysis of stroke 5). Specifically, we were interested in whether movement parameters would differ when comparing conditions that require the same movements but have different visual characteristics. Movement times in the gain change condition were more homogeneous than in the target change condition—that is, short movements were slower and long movements were faster in the gain change as compared to the target change condition. Movement times in the target + gain change condition were positively related to visual amplitude. Both results indicate that the visual context is important to the control of movement. The influence of visual context was also observed in peak velocity. Short visual amplitudes resulted in the highest peak velocities (coinciding with shorter movement times).

Experiment 2 was conducted as a control experiment to rule out that the effects observed during adaptation in Experiment 1 were due to the possibility that adaptation may have been incomplete in stroke 5 and to provide further evidence that Fitts' law does not account for the observed effects. The results indicated that effects of extracorporeal space on movement kinematics are also observable when participants have a relatively long time to adapt. Systematic differences in movement time were obtained, even though they should be the same according to Fitts' law.

Compensation

For Experiment 1, we predicted that compensation onset for gain changes should occur later than for target

changes. This prediction was confirmed. In the former case participants needed to detect a discrepancy between an internally predicted and an observed location on the screen; this information needed to be accumulated. In contrast, target changes could be detected immediately. There was also some evidence that compensation for larger changes occurred earlier than compensation for smaller changes. This is presumably due to the fact that sensory feedback is noisy, thereby making contexts that have large sensory differences easier to distinguish than those with similar sensory feedback (Vetter and Wolpert 2000). However, one might argue that larger changes were compensated for in a more drastic manner, and that they are therefore detected earlier by our statistical procedure. We tried to avoid this problem by using a nonparametric statistical method to determine the compensation onsets. There is also the possibility that the faster compensation of larger changes is strategic—because they require more drastic adjustment, there is more pressure to compensate for them and therefore this is done earlier. The result that reductions (in both, visual amplitude and required movement) lead to faster compensation than extensions can also be interpreted in this way. There is a higher necessity for fast compensation in reduction conditions, since not doing so irrevocably leads to overshoot errors. In the extension conditions, however, there is less pressure to compensate quickly.

We also predicted that, even though participants would try to compensate for the introduced changes, the extent to which immediate adjustments are possible should be limited. Thus, predictable aftereffects of the previous stroke should be observed. This was indeed the case. The aftereffects consisted of over- and undershoot, depending on whether a shorter or longer movement was required, and a specific pattern of movement times.

The present results are in accordance with previous studies of reaching, demonstrating that humans construct motor commands based on a prediction of forces that will be experienced in the upcoming movement (Shadmehr and Mussa-Ivaldi 1994). The CNS stores the values of specific parameters that determine the relationship between movements and their appearance in external space in memory. Movement reproduction therefore depends on information about control variables stored and recalled from memory, or, depending on the task, in short-term memory (Scheidt et al. 2001). When new forces or perturbations are imposed, the prediction is in error and the arm does not follow the desired trajectory (aftereffect). With practice the motor commands are modified and the trajectory approximates the desired path (adaptation) (Shadmehr and Mussa-Ivaldi 1994; Thorougman and Shadmehr 2000).

Adaptation

In Experiment 1, the main question we were concerned with was whether there would be an influence from

different visual environments when the movements required were actually the same after participants had adapted to the new condition. This was the case; different visual amplitudes (with equal movement amplitude) resulted in significantly shorter or longer stroke durations. Furthermore, conditions with lower gain had a higher peak velocity and conditions with higher gain had a lower peak velocity. Likewise, in Experiment 2, in which participants were able to adapt to a certain mapping for a longer period of time, we obtained different movement times for conditions which differed in visual space, but were equal in movement space. As in Experiment 1, movements with higher gain were slower and had correspondingly lower peak velocities than movements with lower gain.

The present results thus provide strong evidence in support of the hypothesis that the CNS plans visually guided movements in a perceptual (visual) frame of reference (Flash and Hogan 1985; Goodbody and Wolpert 1998; Hogan and Flash 1987; Wolpert et al. 1994; Flanagan and Rao 1995; Mechsner et al. 2001). Previous studies have often investigated curvature of movement (Wolpert et al. 1994; Flanagan and Rao 1995). We were able to show that the role of vision generalizes to other aspects of movements (movement amplitude) as well. Thus, the present results considerably strengthen the argument that planning occurs in visually perceived space, which seems to be the natural frame of reference for movement planning.

Fitts' law cannot explain the observed effects; the fit was not very good when conditions differed in gain in Experiment 1. We further ruled out Fitts' law as an explanation for the observed results in Experiment 2. Here we obtained systematic differences in movement times even though movement times should have been the same according to Fitts' law. These results are supported by a study in which different gains were fitted with separate Fitts' functions, and those functions differed from each other (Kantowitz and Elwers 1988). This implies that Fitts' law can be applied within a certain gain condition, but not across gains.

The results of our study are in accordance with a previous study by Rosenbaum and Gregory (2002). In this study, visual demands were kept constant while motor demands were varied. Movements were performed at a given frequency. The results showed that accuracy was more difficult to control at higher gains. Although there was no requirement to produce equal movement frequencies in the present study, the results obtained by Rosenbaum and Gregory (2002) suggest that movements with higher gain should be slower than movements with lower gain, to compensate for the higher difficulty. This prediction is in accordance with the results of the target+gain change condition in Experiment 1 and with Experiment 2. There, participants always needed to carry out the same movement, but the observed visual amplitudes differed. At smaller visual amplitudes, which also implies a small gain, participants were faster than at longer visual amplitudes,

which have a large gain. These results were backed up by the comparison of the target change condition with the gain change condition in Experiment 1. Reduced movements were slower in the gain change condition (higher gain) than the target change condition, and extended movements were faster in the gain change condition (lower gain) than in the target change condition. One could thus assume that the priority of perceived consequences for the organization of motor behavior serves the objective of maximizing the predictability of the trajectory (Flash and Hogan 1985).

The present results suggest that movement planning is not only based on minimization of cost functions associated with movement production, but that movement planning is mainly optimized with respect to the consequences perceived in extracorporeal space. The movements were, however, only partially determined by the visual reference frame; the required movement amplitude did also have an effect on the movement parameters. One explanation for this effect could be that there are two sources that can be used to judge the kinematics of the movement: vision and proprioception. Conflict between the two senses may limit adaptation to be solely based on visual coordinates. It has previously been found that both visual and kinesthetic information about the location of the hand is used (Goodbody and Wolpert 1999). However, since we manipulated only amplitude, which is basically a size transformation, it is unlikely that participants still experienced a conflict when they were already adapted to the new situation while drawing the fifth stroke in Experiment 1. It has been shown that visuomotor mappings of simply scaling size are quite easy to adapt to (Bedford 1994). Transformations of shape, as used in other studies (Goodbody and Wolpert 1999) are more difficult to acquire (Bedford 1994), and more likely to produce conflict. Furthermore, proprioception is not very accurate in predicting hand position (Ghilardi et al. 1995), and proprioceptive feedback might even be reduced during the adaptation to visuomotor transformations (Jones et al. 2001).

The influence of movement amplitude might be best explained by the fact that the control of movement in extracorporeal space is limited by the structural constraints from the inherent characteristics of the body as a mechanical system. If movement speed exceeds a certain (comfortable) range this poses a constraint on the kinematics. Knowledge of the neuromuscular constraints therefore ought to be used in movement planning. Dynamic aspects of a movement are limiting factors of movement organization with reference to extracorporeal space.

Although it has previously been assumed that movement planning occurs in "extracorporeal space" (Flash and Hogan 1985), differentiation between the kinematics of body parts and the behavior of a tool in external space has rarely been made (but see Flanagan and Rao 1995; Wolpert and Flanagan 2001). Our results for the adaptation phase in Experiment 1 and the results

of Experiment 2 point to the importance of differentiating between the kinematics of body parts and the movement representation in extracorporeal space. This is in agreement with the view that the current context is estimated in movement planning (Vetter and Wolpert 2000). According to this view, the CNS estimates properties of objects in the world and prevailing environmental conditions in order to enable successful movement planning. Context estimation requires the CNS to construct and use two types of internal models: it needs to simulate the behavior of both the body and the outside world (Vetter and Wolpert 2000). We agree with this view. However, the critical question is which level provides the main reference frame for movement planning. In accordance with the ideomotor principle, we suggest that distal consequences and context of movements provide the main reference frame (Hommel et al. 2001; Prinz 1992, 1997). In other words, we assume that movement representation in the external world is on the highest level of a hierarchical structure of movement planning. Context estimation is then used to translate those external representations into lower levels, like body part kinematics and dynamics.

This assumption seems to be necessary to explain phenomena like tool use. A necessary precondition for tool use is the ability to acquire flexible mappings between movements and their consequences (Imamizu et al. 2000) and to make the effects achieved in the environment the primary instance of control (Mechsner et al. 2001). The ability to control movements in reference to distal effects, like the visual feedback in our task, presents a special and highly adaptive instance of motor control, without which we would be unable to perform many everyday tasks. As soon as not the movement itself is the aim of our actions, the distal reference frame will be used to guide our movements.

General conclusion

In summary, we found that the compensation for unpredictable changes in the environment produces predictable aftereffects of the previous movement. Adaptation to changes occurred in reference to distal effects in extracorporeal space. This effect was obtained with both relatively short-term and relatively long-term adaptations. This supports a hierarchical view of movement organization and planning, in which distal movement representation is the primary frame of reference.

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