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RESEARCH NOTE

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Transfer of sensorimotor adaptation between different movement categories

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Abstract It is well known that sensorimotor adaptation will transfer from the practiced to the unpracticed arm, which has been taken as evidence that adaptation is located in the brain before the divergence point for left and right arm control. We now explore whether adaptation will transfer between different movement categories as well. Subjects were exposed to a 60-deg visual rotation first in a tracking and then in a pointing task, or vice versa. We found a substantial transfer of adaptation between tasks, but its magnitude was larger from pointing to tracking than from tracking to pointing. This benefit of pointing persisted when the use of cognitive strategies was minimized by a concurrent, attention-demanding task, but it was lost when pointing amplitudes were very small. We conclude that adaptation is located in the brain before the divergence point for different movement categories, and that movements with a large ballistic component facilitate adaptation transfer.

Keywords Motor learning · Sensorimotor adaptation · Manual tracking · Manual pointing · Transfer

Introduction

When subjects are exposed to a visually or mechanically distorted environment, their sensorimotor performance is initially disrupted, and then gradually returns to normal (Stratton 1897; Kohler 1955; Shadmehr and Holcomb 1999). Experimental evidence suggests that this seemingly uniform adaptive improvement is actually brought about by several distinct processes. One of them is the compensatory recalibration of the brain's sensory-to-motor transformation rules, which might be called "genuine" adaptation. However, improvements can also be obtained by so-called "strategic processes," such as movement corrections based on sensory feedback, and/or cognitive schemes which supersede the non-adapted transformation rules (Redding and Wallace 1997; McNay and Willingham 1998). Strategic processes and recalibration are typically separated out by tests of retention, transfer, or interference with another task: The former are thought to dissipate quickly after the end of exposure, while the latter is stored in long-term motor memory, from where it can be activated days or weeks later (Lazar and van Laer 1968; Shadmehr and Brashers-Krug 1997; Bock et al. 2001).

Sensorimotor adaptation is not limited to the specific movements which subjects executed during the adaptation period, but rather generalizes to untrained directions (Bock 1992), amplitudes (Bock and Burghoff 1997), and parts of the workspace (Shadmehr and Moussavi 2000). Adaptation also generalizes to the untrained hand (Cunningham and Welch 1994; Imamizu and Shimojo 1995), and this intermanual transfer has been taken as evidence that the adaptive mechanism is located in the brain upstream from the point where the processing pathways for the left and the right arm diverge.

Little is known about another kind of adaptive transfer, namely that between different movement categories. Assume that a subject adapts to a distortion while executing *tracking* movements, and is then asked to execute *pointing* movements under the same distortion: If we find that adaptation transfers easily between these two movement categories, we could conclude – as in the above intermanual work – that the underlying mechanisms are located upstream from the point where the pathways for pointing and tracking diverge; otherwise, we could conclude that adaptation is movement-type specific.

The purpose of the present work was to investigate the transfer of adaptation between movement categories, and thus to contribute to our knowledge about the localization of adaptive mechanisms within the sensorimotor system.

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Materials and methods

We used the same experimental apparatus as in our previous studies (e.g., Abeele and Bock 2001a), shown schematically in Fig. 1. In brief, participants watched a vertical back-projection screen (S) through a tilted mirror (M), such that it appeared in a horizontal plane (H). Because of the mirror, subjects were unable to see their arm; however, the position of their right index fingertip was registered by the Fastrak motion analysis system, and displayed to them as a cursor on the screen. The Fastrak is based on electromagnetic induction, and has a spatial and temporal resolution of 1 mm and 8 ms, respectively.

Manual tasks

Each subject was tested with two manual tasks. The *tracking* task replicated our previous work (Abeele and Bock 2001a, 2001b): A red circular target of 1 cm diameter moved along a complex path, and subjects were instructed to follow it with the cursor as accurately as possible. Tracking episodes of 50 s duration were separated by pauses of 1–2 s, self-terminated by the subjects. Performance was quantified conventionally as root mean square error (RMSE) between target and cursor position within each tracking episode, disregarding the first 500 ms of each episode, to minimize artifacts due to initial hand positioning.

The *pointing* task closely replicated the center-out task of Krakauer et al. (2000). A 1-cm starting point was presented in the center of the screen, and 1-cm targets appeared at 12 cm distance from it, in one of eight randomly selected locations. Each target appeared for 1.5 s, and subjects were instructed to move the cursor during this time to the target and back in a smooth, uncorrected movement. Pointing episodes were also 50 s long, and thus allowed the execution of 33 movements. Again, self-terminated pauses of about 1–2 s duration were used.

Pointing performance was quantified as the mean angular error between target direction and initial hand direction in each episode, disregarding the first movement per episode. The initial hand direction was determined by an interactive computer routine, as the direction of a line connecting the hand position at movement onset to that at peak velocity; the algorithm had to be hand adjusted in less than 5% of cases. This error measure is largely unaffected by corrective adjustments, which occur during later phases of the movement.

At the end of each 50-s episode, the respective error score was displayed to the subjects as an incentive.

Procedures

We first determined each subject's baseline performance during five episodes of tracking, and five episodes of pointing movements, while the cursor provided *veridical* visual feedback about the momentary position of the fingertip. Visual feedback was then transformed by a 60-deg clockwise rotation about the display center; thus, when subjects now moved their finger straight left, the cursor moved to the left and forward; when they moved the finger straight forward, the cursor moved forward and right, etc. The proper compensation for this distortion is achieved by rotating the motor output by 60 deg counterclockwise with respect to the visual input. Under this rotated visual feedback, subjects executed first one manual task for 15 episodes, and then the other manual task for another 15 episodes.

Before subjects were exposed to rotated vision, we described and demonstrated the effect of this manipulation to them, and instructed them "Don't try and mentally figure out the rotation; just use visual guidance to follow the target. The task may seem difficult at first, but you will find that you improve with practice."

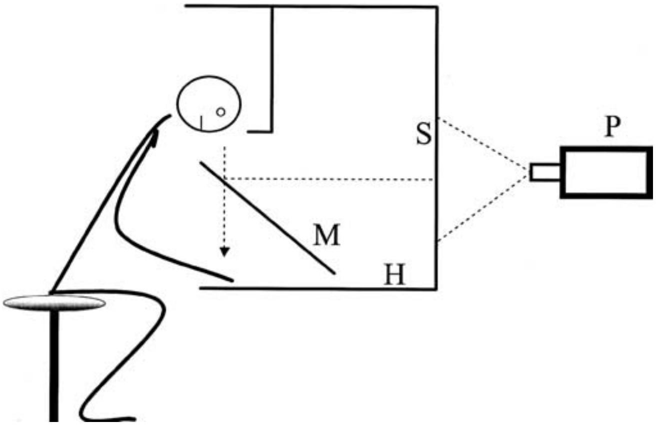

Fig. 1 Schematic view of the setup, showing a subject in front of the back-projection screen (*S*), watching it through a mirror (*M*) tilted at 45 deg. The projected (*P*) image appeared in a horizontal plane (*H*), which was also the plane of hand movement

Subjects

Forty human volunteers (22 males and 18 females) participated in our study. They were all university students, aged 20–28 years, naive as to the purposes of our study, right handed, and exhibited no overt sensory or motor deficits except for corrected vision. They signed their informed consent to this study, which was part of an experimental series preapproved by the authors' local Ethics Committee. Subjects were randomly subdivided into four groups of 10, and each group received a somewhat different experimental protocol (see "Results").

Results

The top part of Fig. 2 shows the error scores of a participant from Group A, and another from Group B. Subjects in Group A executed first 15 episodes of tracking and then 15 episodes of pointing movements; this order was reversed for subjects in Group B. The leftmost part of each subject's graph shows baseline data, collected under normal visual feedback. Following visual rotation (dashed line), the errors increased substantially, and then gradually returned towards the baseline. This is typical adaptive behavior, as previously observed in a large number of studies. Further from Fig. 2, the errors increased again when subjects switched from one movement category to the other, and then returned once more towards the baseline. Most importantly, the second increase was *considerably smaller* than the first, for both subjects. It therefore appears from Fig. 2 that adaptation was easier when subjects have previously adapted to the same visual distortion using another movement category, i.e., that adaptation transferred between categories.

The bottom part of Fig. 2 illustrates the mean error scores of all subjects in Groups A and B. The data are arranged differently than in the top part of Fig. 2, such as to allow a comparison of adaptation in naïve and in pre-exposed subjects. The results show that pointing performance in subjects which previously adapted in a tracking task (Group A) was better than that in naïve subjects

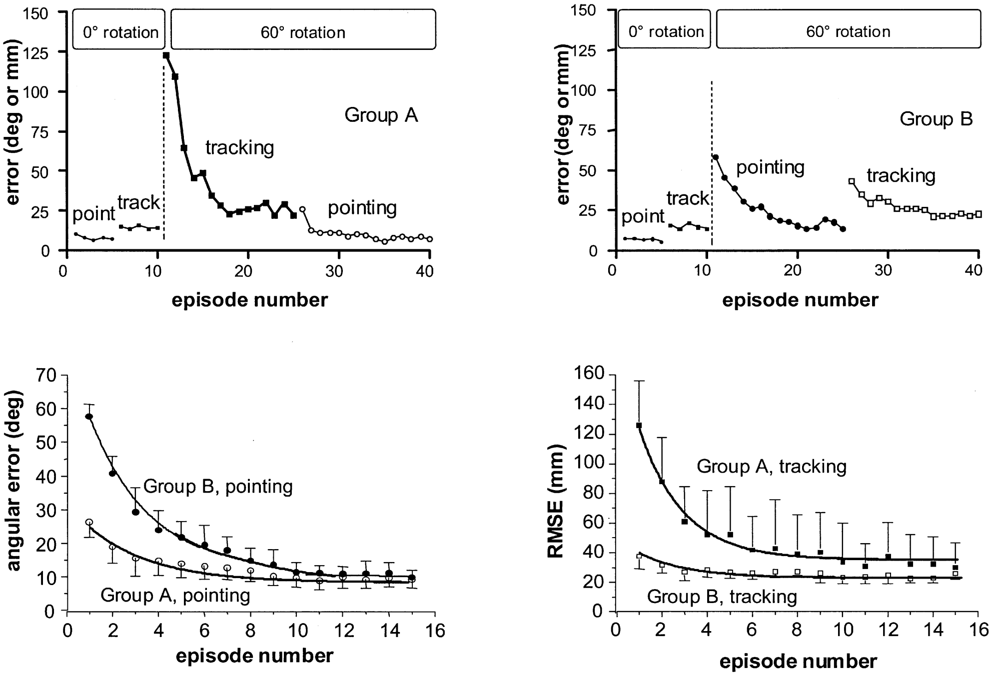

Fig. 2 *Top* Performance errors of a subject from Group A and Group B, respectively. Each data point represents the mean error of that subject for the given experimental episode. Movement categories and visual feedback condition are indicated in the graphs. *Bottom* Performance errors across subjects while pointing (*left graph*) and while tracking (*right graph*). *Symbols* represent across-subject means, and *bars* standard deviations; *filled* symbols correspond to naïve, and *open symbols* to pre-exposed, subjects. *Curves* are exponential fits to visualize trends; the fitted time constants were 2.56 (B, pointing), 2.77 (A, pointing), 2.77 (A, tracking) and 2.03 (B, tracking) episodes

(Group B); accordingly, tracking performance in experienced subjects (Group B) was better than in naïve ones (Group A). These differences were strongest for the initial episodes, and gradually decreased later during adaptation. These observations were confirmed by analyses of variance (ANOVAs), using the between-factor Task, and the within-factor Episode: For the data in either graph, we yielded a significant effect of Task ($F_{(1,9)}$=35.4 or 10.3, respectively; P<0.05), Episode ($F_{(14,126)}$=201.1 or 40.4, respectively; P<0.001), and their interaction ($F_{(14,126)}$=47.2 or 24.3, respectively; P<0.001).

It appears from Fig. 2 that the *magnitude* of transfer from pointing to tracking (right graph) is larger than that from tracking to pointing (left graph). However, a direct comparison is problematic, since pointing and tracking errors are expressed in different units, and the baseline values are different. We therefore decided to express the magnitude of transfer in normalized scores, using:

$$\mathrm{Transfer}(\%) = 100 - (\mathrm{I_P} - \mathrm{B_P})/(\mathrm{I_N} - \mathrm{B_N}) \times 100$$

where B and I denote the baseline error and the initial error at adaptation onset, respectively, and the subscripts N and P refer to data from naïve and preadapted subjects, respectively. Thus, 100% transfer would indicate that the initial error of preadapted subjects did not increase beyond their baseline, and 0% that it was as high as in naïve subjects.

The outcome of this normalization procedure is plotted in the left part of Fig. 3. The magnitude of transfer from tracking to pointing in Group A was about 60%, and that from pointing to tracking in Group B was about 80%, which is significantly larger (one-way ANOVA: $F_{(1,18)}$=28.99, P<0.001). Our data therefore confirm that the magnitude of transfer from tracking to pointing is indeed higher than in the other direction.

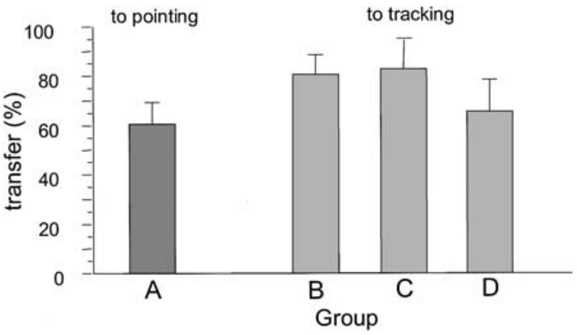

Fig. 3 Normalized magnitude of transfer, calculated according to the formula in the text. *Bars* show the across-subject means and standard deviations for each of the four experimental groups

In order to understand the advantage of the pointing task for adaptation transfer, we modified the pointing protocol of Group C from that of Group B in several ways. First, the visual discordance was not explicitly demonstrated and described, and subjects were merely told that the task would now "become more difficult." Second, subjects' explicit knowledge about the nature of the distortion was assessed by a questionnaire after completion of the experiment. Third, subjects performed a concurrent attention-demanding task while pointing: An electronic device pronounced letters of the alphabet in a random order every 4 s, and subjects responded by spelling out the preceding letter. For example, when hearing "s," they responded "r." Since 25 different letters were used, the success rate of mere guessing was 4%. Across all episodes and subjects, about 1,700 letters were pronounced. This dual-task procedure was practiced with the subjects under normal visual feedback, before onset of the actual experiment.

Subjects produced an average of 68% correct responses in the letter naming task, which is significantly above chance (binomial test: n=1,700, f_{obs}=0.68, f_{exp}=0.04, P<0.001). The questionnaires revealed that only one subject identified the distortion correctly; the others gave comments such as “you made the cursor move in some wrong way, but I don’t know in which.” Figure 3 illustrates that the transfer of adaptation from pointing to tracking was *not* affected by the change of instructions, or by the additional letter naming task; accordingly, a one-way ANOVA yielded that the magnitude of transfer from pointing to tracking was not significantly different between Groups B and C ($F_{(1,18)}$=0.22, P>0.05).

Subjects in Group D were tested with the same protocol as Group B, except that in the pointing task the distance between starting place and targets was reduced from 12 cm to 2.5 cm. This modification was introduced such that the target-cursor distance in pointing became similar to that in tracking. Figure 3 summarizes the outcome: The transfer of adaptation from pointing to tracking was smaller in Group D than in Group B. Accordingly, a one-way ANOVA yielded a significant difference between these two data sets ($F_{(1,18)}$=9.86, P<0.005).

When comparing all four groups by Tukey’s post hoc tests, we confirmed that Group A and D differed from B and C (each P<0.01), B and C were *not* significantly different (P>0.05), and A and B were also *not* significantly different (P>0.05). Thus, adaptation transfer from tracking to pointing in Group A was quantitatively similar to that from pointing to tracking in Group D.

Discussion

The present work documents that adaptation to a 60-deg rotation of visual feedback, achieved with tracking movements, transfers substantially to pointing movements (Group A); similarly, we found a strong transfer of adaptation from pointing to tracking (Group B). It therefore seems that the neural substrate of adaptive change is accessible by different movement categories. Following the arguments of Imamizu and Shimojo (1995), we interpret this finding as evidence that in our study much of the adaptive change occurred in the brain upstream from the divergence point between pointing and tracking control.

Even more interestingly, the *magnitude* of transfer was significantly higher from pointing to tracking (about 80%) than from tracking to pointing (about 60%), which indicates that adaptation with pointing movements was more efficient. One possible explanation for this outcome is that pointing provided much more compelling cognitive cues about the nature of the imposed distortion: In each pointing response, the difference between a fixed target direction and the actual direction of cursor movement could be appreciated over substantial time, which might have prompted subjects to develop cognitive strategies for adaptation, such as “move the cursor 60 deg past the target.” Once established, such strategies might have remained useful in the subsequent tracking task. In contrast, the relationship between the continuously changing directions of target and cursor in a tracking task may not be that easily appreciated, which could make it more difficult to establish cognitive strategies.

The above interpretation was scrutinized in Group C. Subjects were not informed about the nature of the visual distortion, cognitive reasoning was diverted from the pointing task to a concurrent letter-naming task, and subjects’ explicit knowledge about the distortion was largely absent after the experiment. We therefore feel confident that the formulation of cognitive strategies was not very accomplished in Group C. Still, we found that the transfer of adaptation from pointing to tracking in Group C was not smaller than in B. This outcome suggests that the advantage of pointing is not strongly related to a deeper cognitive processing during the pointing than during the tracking task.

As an alternative interpretation for the advantage of pointing, it is conceivable that pointing movements do not invite vision-based corrections to the same extent as do tracking movements. Aimed arm movements consist of “ballistic” components, executed in an open-loop fashion, as well as “current control” components, which rely on sensory feedback (Woodworth 1899; Craik 1947); ballistic components bring the hand into the vicinity of the target, and the final corrections are then performed under sensory feedback (Greene 1972). Since the target-cursor distance was typically smaller in our tracking than in our pointing task, tracking might have encouraged corrections based on visual feedback. Even though such corrections will not be fully compensatory due to the presence of a visual distortion, they will still bring the hand closer to the target, and thus improve subjects’ performance during adaptation.

The above view was scrutinized in the subjects of Group D by dramatically reducing the required amplitude of pointing. We selected a value of 2.5 cm, since this was about the smallest amplitude which still allowed a meaningful analysis of initial movement direction. In accordance with our hypothesis, we found that adaptation transfer from pointing to tracking in Group D was no longer superior to that from tracking to pointing in Group A. This outcome is probably not related to the fact that pointing movements in Group D were limited to a small part of the workspace, since adaptation was shown to fully transfer to untrained workspace areas (Bedford 1989; Bock 1992), also when adapting to a visual rotation (Krakauer et al. 2000). Instead, our findings are in agreement with the view that large-amplitude pointing movements produce more sensorimotor recalibration and less feedback-based corrections than do small-amplitude pointing or tracking, and therefore yield a stronger transfer of adaptation (80% vs 60%).

In conclusion, the present work not only documents that sensorimotor adaptation will transfer substantially between movement categories; it also illustrates that improved performance during an adaptive session is not exclusively due to sensorimotor recalibration. The contribution of additional mechanisms can be elucidated by the approaches taken in our Groups C and D, but also by studying the aftereffects of adaptation, long-term retention, or the interference between non-compatible distortions (Krakauer et al. 1999; Shadmehr and Holcomb 1999; Bock et al. 2001). Finally, the present data indicate that research on sensorimotor recalibration should focus on movement types with a strong ballistic component – such as large-amplitude pointing, or ball throwing – since such movements seem to favor recalibration over feedback-based corrections.

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