Knowledge of Performance is Insufficient for Implicit Visuomotor Rotation Adaptation

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Abstract

The ability to adapt is a fundamental and vital characteristic of the motor system. In the present study, we altered the visual environment and focused on the ability of humans to adapt to a rotated environment in a reaching task, in the absence of continuous visual information about their hand location. Subjects could not see their arm but were provided with post trial knowledge of performance depicting hand path from movement onset to final position. Subjects failed to adapt under these conditions. We sought to find out whether the lack of adaptation is related to the number of target directions presented in the task, and planned two protocols in which subjects were gradually exposed to 22.5° visuomotor rotation. These protocols differed only in the number of target directions: eight and four targets. We found that subjects had difficulty adapting without the existence of continuous visual feedback of their performance regardless of the number of targets presented in task. In the four target protocol, some of the subjects noticed the rotation and explicitly aimed to the correct direction. Our results suggest that real time feedback is required for motor adaptation to visual rotation during reaching movements.

Keywords: Visuomotor rotation adaptation • Motor learning • Reaching movements • Knowledge of performance • Visual feedback.

Introduction

When trying to reach a visual target, the human motor system transforms information about the target location into a set of motor commands that produce muscle activation and joint torques. In order to achieve such a complex transformation, the motor system must have access to the parameters of the arm as well as the controlled environment. Naturally, both our body and the environment we interact with undergo changes, and the ability to adapt is crucial for performing accurate movements in natural time varying environment (Shadmehr and Wise 2005).

It is important to note that unlike skill acquisition, motor adaptation does not enhance the motor system's capabilities overall, but changes the system to a different state of performance. It can be simply described as the recovery of performance within the changed environment. It follows that in order to maintain a desired performance, the motor system has to be robust to changes, and this robustness is believed to be achieved through an updating, or adaptation, of an internal model that can predict the motor commands required for a specific task (Kawato 1999; Karniel 2009). After a period of training, the internal model based controller adapts and produces the desired movement.

Adaptation has been broadly studied using different tasks, some involved a change in the visual environment, such as a shift or rotation (Pine et al. 1996; Baraduc and Wolpert 2002; Krakauer et al 2004; Wang and Sainburg 2005; Bernier et al 2005; Mazzoni and Krakauer 2006), and some involved mechanical perturbations in the environment dynamics, e.g., force field (Shadmehr and Mussa-Ivaldi 1994; Fine and Thoroughman 2006; Wagner and Smith 2008). In both cases, exposure to a novel environment is usually characterized by initial large errors followed by incremental improvements in task performance. The later phase is referred to as the adaptation phase.

Current understanding of the motor system asserts that sensory prediction error, namely, the difference between the actual and the expected sensory feedback for a given motor command, drives trial by trial adaptation (Thoroghman and Shadmehr 2000; Donchin et al 2003; Tseng et al 2007). However, this learning mechanism might depend on the timing in which the prediction error is available. Previous studies have demonstrated that subjects can adapt to visuomotor rotation when performing visually guided movements, i.e., when a full continuous visual feedback of a cursor is provided while the hand is moving towards the target (Krakauer et al 2000; Tseng et al 2007). In this case, the discordance between proprioceptive feedback and visual feedback could be detected during task execution. Furthermore, several studies suggested that subjects can adapt to a rotated environment when visual feedback is provided after task execution, i.e., knowledge of performance depicting cursor path from movement onset to final position (Pine et al 1996; Hinder et al 2010), or cursor end point (Scheidt and Ghez 2007), is presented following task execution. In a series of preliminary studies aimed at exploring feedback and feedforward adaptation we have recently failed to obtain visuomotor adaptation based on knowledge of performance without any real time feedback (Peled et al 2010; Peled and Karniel 2010). In these studies we used 16 and 8 target setups correspondingly with similar results of lack of adaptation. We were puzzled by this result and considered the possibility that the number of targets and the extent of training might be the reason for the lack of adaptation in our preliminary studies. Therefore here we tried also four targets and extended training protocols.

Previous studies have shown that reaching movements are represented in the motor system as intended direction and distance from a given starting point (Krakauer et al 2000), and that adaptation to visuomotor rotation remaps this representation (Wang and Sainburg 2005). It also has been shown that the rate of adaptation decreases when the number of target directions is enlarged (Krakauer et al 2000). Nevertheless, all these rotation adaptation results were collected from visually guided reaching movement studies. In this study we further investigate the rotation adaptation process, and focus on the difference between online visual feedback and knowledge of performance in a reaching movement task. We also seek to learn about the relationship between the number of target directions and human's ability to adapt in these conditions.

Two groups of subjects were exposed to a 22.5^0 visuomotor rotation under the same conditions except for the type of visual feedback provided. One group of subjects was provided with full continuous feedback of the cursor (CF), while the second group was provided with knowledge of performance depicting the full cursor path (KP). If the information of sensory prediction error is sufficient for trial by trial adaptation to occur, we expect to see no difference in the performance of the two groups. However, our results show clear dichotomy between the two groups and therefore suggest that trial by trial adaptation might involve more complex mechanisms that require a real-time feedback policy in addition to the knowledge of performance.

Methods

Subjects were asked to perform planar point to point reaching movements under a gradually incremented visuomotor rotation, as detailed below.

Subjects

Twenty eight right-handed naive subjects (aged 22-30, males) were paid to participate in the experiments. As stipulated by the local Helsinki committee, subjects signed informed consent forms to participate in the experiments conducted at the Computational Motor Control Laboratory at Ben-Gurion University of the Negev.

Experimental apparatus

We used the *SensAble* 3D virtual reality system for performing the experiment. The subject holds a robotic arm (*SensAble* PHANTOM® Desktop™ Haptic Device) which produces a sense of touch in a 3D scene graph computer simulation. Subjects were seated in a high chair, facing a 19" computer LCD screen positioned at eye level, and asked to wear an orthopedic wrist brace in order to stabilize their wrist during the task. Their right arm was supported against gravity by a custom made air-sled which was attached to a 30-psi compressed air source, and provided essentially frictionless motion of the arm in the horizontal table plane (figure 1a). In addition, a virtual horizontal surface, parallel to the table desktop, was rendered in the virtual environment in order to assure horizontal movements only. The surface was invisible but could be felt when touched by the robotic arm, i.e. the robotic arm could not cross the virtual surface and subjects moved their hand while the robotic arm smoothly slid on the rigid virtual surface (frictionless movement). Direct visual feedback of the hand and the robotic arm was prevented by a blue cloth that covered subjects’ shoulders and arms. Instead, subject’s hand position was tracked by the robotic arm, and translated to a 0.3cm radius white sphere on the screen, providing visual feedback of hand location in real-time. This setup assured subjects could only rely on the visual feedback provided on the screen, and their proprioceptive feedback. Position and time were sampled at 200Hz by the robotic arm.

General task description

This report describes three protocols of experiments. The first and second protocols differ only in the number of targets (eight and four targets respectively, figure 1b). The first and third protocols differ in length of the experiment, i.e., in the number of blocks (see *Experimental Paradigm* below). In all protocols subjects were required to perform point-to-point reaching movements in the horizontal table plane. Each movement started at a 0.4cm radius ring located at the center of the screen, and ended at one of 0.5cm radius red targets evenly distributed on a 10cm radius circle. On each trial, only one of the targets appeared randomly on the screen.

Subjects were instructed to start their movement as soon as the target appears on the screen, move smoothly towards the target without pausing, and stop at the target location. At the end of each movement, subjects were provided with knowledge of results feedback (KR), which concerns information about the outcome of an action. The KR feedback we provided referred to movement success (i.e., hitting or missing the target) and movement velocity. A message based on the time elapsed from target appearance to movement stop was presented on the screen for 1.2sec: “Excellent!” for movements that last 0.9-1.1sec, “Too slow!”, and “Too fast!” for slower and faster movements respectively. Note that the durations mentioned here are calculated with respect to target appearance and not movement onset. Furthermore, if the cursor hit the target (the criteria for hitting the target was a final end point of the cursor within a 1.5cm radius circle around the target), the target’s radius would grow from 0.5cm to 2cm, and its color would change to reflect movement duration: red for too fast (i.e., no change in the color), blue for too slow, and green for a good duration movement. In case the target was missed, subjects were not cued explicitly. Instead, the final location of the cursor remained on the screen for additional 1.2sec, allowing them to see their exact end point relative to the target location.

In the last case, the text message displayed on the screen for a good duration movement was 'Good velocity!' instead of 'Excellent!' in order to encourage subjects to hit the target. Subjects were instructed to get as many 'Excellent!' movements as possible (i.e., hitting the targets in a time window of 0.9-1.1sec), and were provided with a score at the end of each block, which was calculated as the percentage of 'Excellent!' movements in that specific block.

Each trial terminated either when hand velocity was below 0.4m/sec for more than 0.1sec, or when trial duration lasted longer than 3sec. In the last case, “Out of time!” message appeared on the screen and the trial was repeated to the same target. All subjects were allowed to correct their path while moving towards the targets, but most of them did not make any noticeable corrections since real time visual feedback of the cursor was not available during movement execution. When a trial ended, after duration of 1.2sec in which performance feedback was displayed on the screen, subjects were asked to return their hand back to the starting ring without visual feedback of the cursor (the starting ring was displayed on the screen at all times). Assistive force was then activated by the robotic arm in the direction of the starting ring (rendered as a spring with K=20N/m), in order to help the hand to find its way back. When cursor position reached the starting ring, the ring color would change to green, and subjects were asked to hold their hand in place. Only after the cursor had been inside the ring for 1sec, a new target appeared on the screen, and a consecutive trial began.

Experimental groups

In the *eight target protocol*, twelve subjects were randomly assigned to one of two groups (n=6 per group) that differ in the type of visual feedback about the task performance. Note that knowledge of performance feedback (KP) provides information about the spatiotemporal characteristics of the action itself, regardless of its outcome. The first group (control) was given a full continuous visual feedback (CF) of cursor position over the whole work space during movement execution, while the second group was provided with only KP feedback depicting the cursor path from the starting ring to its final position. The KP feedback was presented immediately following movement termination for a period of 1.2sec before the assistive forces of the robotic arm were activated. Both CF and KP groups could see their exact end point relative to the target location. Note that both groups were provided with identical KR feedback, but differed in the type of KP feedback (see "General task description" in "Methods" for KR feedback description).

In the *four target protocol*, ten subjects were provided with KP feedback, precisely as described in the second group of the *eight target protocol*, but performed movement to four target instead of eight (figure 1b)

In the *eight target extended training* protocol, six subjects were also provided with exactly the same KP feedback as described in the second group of the *eight target protocol*, but performed a longer learning phase (eight training blocks instead of five).

Experimental paradigm

The experiment was divided into two phases and each phase was divided into blocks of 88 radial movements (table 1). On each block, trials were performed in full ‘cycles’ according to the number of targets in the task, one trial for each target direction. The order of targets presentation within each ‘cycle’ was pseudo-randomized such that all subjects performed the same sequence.

First phase: Baseline, was identical in all three protocols and consisted of two blocks: 'a1', and 'a2'. Hand movements were mapped normally to the motion of screen cursor (figure 1c). Block 'a1' was a warm up block in which online feedback of the cursor position was available to both CF and KP groups. The purpose of this block was to ensure all subjects understood how to produce accurate movements and reach while using the robotic arm. For the KP group it also enabled subjects to appreciate the magnitude of hand movement in each direction before the elimination of the continuous visual feedback in block ‘a2’.

Second phase: Learning, was identical in the *eight and four target protocols* and consisted of five blocks ('b1'-'b5') in which counterclockwise (CCW) visuomotor rotation was introduced (i.e., screen cursor was rotated around the center of the start location). For example, if a 22.5° rotation was applied, hand movement to the right would result in a cursor movement to the up-right in a 22.5° angle (see figure 1d). In order to prevent subjects from explicitly noticing the hand-cursor relationship, the rotation applied in the *Learning phase* incremented gradually such that every 76 trials the rotation increased by 4.5° to a maximum of 22.5° (see table 1). In the *eight target extended training protocol*, the *Learning* phase was longer than the first two and consisted of eight blocks ('b1'-'b8'). The first five blocks ('b1'-'b5') were identical to the design of the eight and four target protocols, whereas each of the last three blocks ('b6'-'b8') was designed exactly like block 'b5' (see table 1), i.e., subjects continued reaching under a full 22.5^0 visuomotor rotation.

After completing all the stages of the experiment, all subjects were asked the exact same questions. The first question was a general question – "Did you notice anything unusual during task executions?" and after their reply another leading question was introduced: "Did you notice any special relationship between the movement of your hand and the movement of the screen cursor?".

To conclude, the *eight and four target protocols* consisted of seven blocks (616 trials in total) and lasted ~70 min, and the *eight target extended training protocol* consisted of ten blocks (880 trials in total) and lasted ~90 min. In all protocols there was a brief break (<1min) between consecutive blocks in which subjects remained seated in their chair and waited for the next block to begin. Although they had been given the option to take a five minutes break between consecutive blocks in case of fatigue, subjects usually did not take more than one break for the entire experiment. None of the subjects has been told about the rotation nor been given any clues about the hand-cursor movement relationship.

Data analysis

Directional error, θ, was determined to be the angle between the vector defined by the start and target positions, and a second vector that was calculated as follows: for each movement we found the peak tangential velocity sample, and took a window of 20 trajectory samples (100ms of movement) such that the peak tangential velocity sample was centered in the middle of the 20 samples window. A simple linear regression over these 20 samples provided the second vector. The angle between the two vectors yielded the trajectory slope and the desired directional error angle. The directional error depicted here assessed feedforward performance, since it is generally accepted that online correction of rapid hand movements are taking place after the peak velocity.

Phase residual error was calculated as the averaged directional error of the last 32 movements of the phase. This measure was used to quantify the extent of adaptation and for comparing between subjects' performance at the end of the baseline and learning phases. Since the data was not normally distributed we used the ranksum test for comparing between the different groups.

All data analysis was performed using MATLAB version 7.6.0.324 (R2008a).

Results

Eight target protocol

Figure 2 shows cursor paths for the CF and KP groups during baseline (left) and learning (right) phases. The grey frames emphasize the hand-cursor relationship in each phase (H and C respectively). Rows 'A' depict cursor paths of a representative subject, whereas rows 'B' depict averaged cursor paths for six subjects. All subjects in both groups produced relatively straight paths along the entire experiment (Figure 2). For the CF group, online corrections ensured that all paths terminated at the desired target, whereas for the KP group, terminal errors remained since online corrections were not available. None of the twelve subjects participated in this protocol reported any explicit awareness to the visuomotor rotation rules. Subjects of the KP group were not able to explain their extensive errors and low success rate, and thought that there was something wrong in their posture or in the accuracy of the system.

Despite the gradual increment in the rotation, the CF group showed minor errors and kept making accurate movements towards the targets (figure 3a). Interestingly, the KP group exhibited increasing errors in the learning phase and could not improve their performance and accuracy in a way that would restore their baseline performance observed in block 'a2' (figure 3b). Note the minor reduction in the errors observed towards the end of block 'b5' which naturally led us to design the *eight target extended training protocol* (see "Discussion"). Figure 3c depicts a comparison of the median of the phase residual error (see "Data analysis") with 95% non-parametric bootstrap CI over the subjects of each group. Even though exposure to the rotation enlarged the directional error in block 'b5' for both groups, the difference did not reach statistical significance for the CF group ($p=0.09$, ranksum test). For the KP group however, the extent of increment of directional error at the end of block 'b5', with respect to the end of block 'a2', was much more salient ($p<0.01$, ranksum test).

Four target protocol

Four out of ten subjects who participated in the *four target protocol* showed poor accuracy when trying to reach for the targets, unlike the other six that were much more accurate (figure 4). Interestingly, the same four subjects reported they did not notice anything unusual during task execution while the other six had noticed the rotation rules and intentionally aimed to the other direction in order to compensate for the perturbation applied. We call these four and six subjects groups 'no strategy' and 'strategy' respectively. Figure 4 clearly demonstrates the difference in performance between the 'strategy' and 'no strategy' groups when visuomotor rotation was applied. Note that one of the 'strategy' group subjects used different strategy compared to the others, and made curved paths towards the targets.

Although both groups showed similar performance till the fourth jump in the rotation increment (i.e., from 13.5° to 18°), the 'strategy' group managed to gradually reduce the errors and compensate for the rotation (figure 5a, 5b). Figure 5c emphasize the difference in performance between the two groups (see figure 3c for comparison details) and demonstrates that the 'strategy' group managed restoring their baseline performance ($p=0.59$, ranksum test) while the 'no strategy' group showed poor performance and large errors compared to their baseline performance ($p<0.05$, ranksum test).

Eight target extended training protocol

In the KP *eight target protocol,* we observed a minor reduction in the errors towards the end of block 'b5' (figure 3b). This observation had led us to design the *eight target extended training protocol,* and add three additional blocks at the end of the *learning phase*: 'b6'-'b8' (see "Discussion"). We call the group of six subjects participated in the *eight target extended training protocol* KP 'extended' group. Figure 6a shows the directional error in each trial of the *eight target extended training protocol* averaged over the KP 'extended' group subjects. It is important to note that three out of six subjects reported that they had noticed the rotation rules and adopted explicit strategy in order to compensate for the perturbation applied. Two other subjects reported that they also used explicit strategy during the experiment, but abandoned it since they were not sure it helps them consistently. Finally, only one subject reported that he did not notice the rotation rules and did not take explicit strategy in order to overcome the perturbation applied. Altogether we found that the longer training did not result in restoring baseline performance (i.e., significant errors minimization), but rather enhanced subjects' awareness to the rotation rules (figure 6b).

Discussion

In this study we found that the existence of sensory prediction error in the form of knowledge of performance is not sufficient to facilitate implicit visuomotor rotation adaptation. Without explicit awareness of the rotation, our subjects failed to adapt to a 22.5° CCW visuomotor rotation in the absent of continuous visual feedback, even when we tried to simplify the task by reducing the number of targets or provided a longer training period.

These findings suggest that rotation adaptation mechanism requires continuous visual feedback in order to be activated, and are not consistent with other studies that reported visuomotor learning when only KP feedback was provided. For instance, Heuer and Hegele (2007) demonstrated learning of direction related visuomotor gains following terminal feedback practice. Some other studies (Kitazawa et al 1995; Bernier et al 2005) introduced a directional bias (shift) between cursor and hand locations and reported that subjects exhibited aftereffects when the perturbation was removed. In addition, Kitazawa et al (1995) illustrated that the rate and amount of directional bias adaptation depends critically on the timing in which the KP is provided, and that the best performance is achieved in the absence of any delay. However, it is important to note that none of these studies involved adaptation to a rotated environment. The perturbation disparity between our study and all the other KP studies mentioned above, and the fact that our subjects did not adapt to the rotation might imply that adaptation to rotation involves different adaptation mechanisms.

A different adaptation study performed by Schiedt and Ghez (2007) showed evidence for KP visuomotor rotation learning. Subjects were asked to reach in a rotated environment without visual feedback of the cursor. After movement termination, the cursor reappeared on the screen and subjects were asked to correct any terminal error by bringing the cursor to target. Even though subjects' compensation for the imposed rotation suggests that this is a good KP rotation learning example, we believe that the correction performed at the end of the movement, while continuous visual feedback of the cursor was provided, and rotation rules were applied, is the key reason for the observed adaptation.

There are two other studies which have probed KP rotation learning in a task similar to our task. In the study of Pine et al (1996), subjects were provided with KP feedback and managed to overcome the rotation implicitly, but performed movements in three directions only: 0˚ (horizontal to the right), 45˚, and 90˚ (vertical upward). We also performed a few studies using a narrow sector of target locations and observed significant improvement in performance (unpublished data). However, all of our subjects who learned the rotation could report the perturbations characteristics when they were asked at the end of the experiment, and we believe that the cause for their awareness was the narrow sector of target locations. In a second study presented by Hinder et al (2010), subjects performed the same task but used different apparatus. Their hand was placed on a manipulandum that allowed movement in two degrees of freedom and helped them controlling the visual screen cursor: elbow flexion/extension resulted in up-down cursor movement, and forearm pronation/supination resulted in left-right cursor movement). Another important difference was that the background color of the display in each block indicated the relationship between the direction of movement and the resulting displacement of the cursor. Therefore, subjects could associate their arm-cursor movement relationship with the contextual cue and use explicit strategies. This might explain why the KP group in their study exhibited exponential reduction in the errors, but did not produce any aftereffects when the perturbation was eliminated. Our finding that real time feedback is required for motor adaptation to visual rotation during reaching movements, agrees with the findings of Hinder et al, and extends them by showing that subjects cannot implicitly adapt even when the task is simplified (i.e., the number of target direction is reduced). Apparently learning a rotation perturbation while reaching in all directions and using only KP feedback is either impossible or much more difficult than learning with continuous real time feedback. This understanding is consistent with Pine et al (1996) observation about the poor rotation learning generalization to different directions.

The *eight target protocol* showed that the group of subjects provided with continuous visual feedback (CF) throughout the movement managed to adapt, whereas the second group of subjects, provided with knowledge of performance (KP) only after movement termination, failed to achieve similar adaptation. This finding is strongly related to the type of feedback, which differed the two groups in two manners: first, the KP group could not get a real time assessment of the cursor location as opposed to the CF group who had the cursor visible at all times.

Second, the KP group had to process during the intra-trial interval not only the KR-related information but also the KP-related information, whereas the CF group only needed to process only the KR-related information. None of the subjects participated in the *eight target protocol* reported any explicit awareness to the perturbation. Since the criteria for hitting the target was a final end point of the cursor within a 1.5cm radius circle around the target, subjects could have made a directional error of about nine degrees without a serious concern. However, in order to perform properly in face of some natural variance in the movement, subjects are implicitly encouraged to aim exactly to the target. Following the results of the *eight target protocol* we suspected that the lack of adaptation of the KP group might be related to the number of targets directions presented in the task. We decided to perform a similar experiment in which only four targets will be presented. This setup allowed subjects to get twice as much exposure to the targets compared to the *eight target protocol* (154 attempts per target compared to 77 attempts per target). We assumed that a CF group will produce similar performance to the one observed in the *eight target protocol*, and therefore decided to test the impact of reduced targets number on the adaptation of a KP group only.

As opposed to Krakauer et al (2000), who showed that when CF feedback is provided, the rate of adaptation decreases proportionally to the increase in the number of target directions, our *four target protocol* results imply that when KP feedback is provided, the reduction in the number of targets does not facilitate faster or easier adaptation, but rather helps subjects to be more aware of the task perturbation, and take different strategies for compensation. A possible explanation can be that the motor system is incapable of generalizing learning to other directions when CF is not provided. This narrow generalization pattern prevents the motor system from using any error experienced in one direction for improving performance in movements made to other directions. A different explanation may be that during CF adaptation one truly learns the rotation, but when KP is provided, it is only possible to learn the motor command required for reaching specific targets, and therefore the number of targets is a major factor. Interestingly, even though subjects in other studies could not use strategies which were explicitly provided by the experimenters (Mazzoni and Krakauer, 2006; Taylor and Ivry 2011), our subjects succeeded using explicit strategy for compensating the rotation. This finding may result from the fact that our subjects formed their own strategies without any verbal instructions. It is possible that self-generated strategies can be more useful than externally-imposed strategies.

When we carefully observed the adaptation curve of the KP group in the *eight target protocol* (figure 3b), we noticed that the errors at the end of block 'b5' might indicate the existence of a slow learning process. We suspected that a longer training session might result in error reduction and performance improvement, and therefore we designed the *eight target extended training protocol* and added three additional blocks at the end of the learning phase: 'b6'-'b8' (see "Experimental paradigm" in "Methods" for blocks design). Nevertheless, we could not find any strong conclusion regarding the ability to learn with a longer practice. Even though the error reduction towards the end of the experiment is salient (figure 6a) it is still far from the adaptation observed with continuous feedback. Moreover, subjects' answers at the end of the experiments imply that the reason for this error reduction is not necessarily an internal implicit process of motor learning but rather a combination of explicit strategies. This finding is consistent with the work of Taylor and Ivry (2011) who demonstrated that a prolonged exposure to a rotation without any feedback influences which strategy subjects use.

Recently Shabbott and Sainburg (2010) performed similar study, in which subjects were exposed to a visuomotor rotation while receiving either CF or KP feedback. Their task differed from ours in a few manners: First, the learning phase (named rotation session in their work) included a 30° clockwise rotation, as oppose to our gradual incremented 22.5° CCW rotation. Second, between consecutive trials performed by the KP group, cursor feedback was restricted to within 2 cm of the start circle, as opposed to our task that prevented any feedback of the cursor. This second difference may be the reason for the partial learning observed in their study. Third, their experiment was shorter than ours - 448 trials compared to our 616 trials. And last, they did not check the effect of reducing the number of targets. Despite the differences mentioned here, Shabbott and Sainburg (2010) obtained similar results. Therefore our study confirms, reinforces, and extends their study.

The motor system employs feedback, adaptation, and learning mechanisms to adjust its motor command to the changing environment (Karniel 2009). This study provides some new information about the boundary between adaptation and skill learning (Karniel 2011), in terms of online feedback vs. KP, and in terms of the awareness to the nature of the perturbation. Our results indicate that KP feedback, as provided in this study, is insufficient for rotation adaptation to occur implicitly. These results suggest that the neural system responsible for motor adaptation to visuomotor rotation requires real time feedback in order to adjust the motor command properly. Further studies are required to put these results in a general context and properly map the function and limitation of the motor system in adaptation and skill learning involved in daily challenges.

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Phase	Block	Num. of trials	Performance feedback		Rotation
			CF group	KP group	(trials)
a (baseline)	a1	88	CF	CF	Null
	a2	88	CF	KP	Null
b (learning)	b1	88	CF	KP	4.5° (1-76) 9° (77-88)
	b2	88	CF	KP	9° (1-64) 13.5° (65-88)
	b3	88	CF	KP	13.5° (1-52) 18° (53-88)
	b4	88	CF	KP	18° (1-40) 22.5° (41-88)
	b5	88	CF	KP	22.5° (1-88)

Table 1 The experimental design. A detailed description of the phases and blocks in the *eight and four target protocols*. The right column shows the rotation value in each block and the graduate increment in the learning phase (in brackets are the relevant trials in each block). Note that the design of the *eight target extended training protocol* included three additional blocks 'b6'-'b8', identical to block 'b5'.

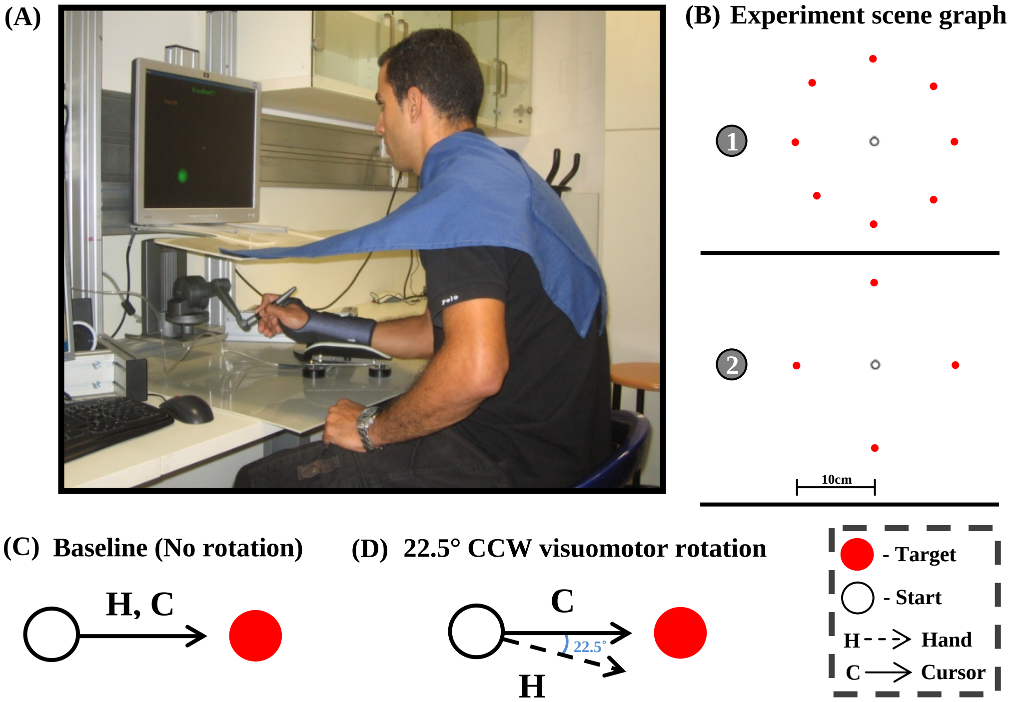


Fig. 1 The Experimental apparatus and task description. **a** The 3D augmented reality system, and the SensAble PHANTOM® Desktop™ Haptic Device. **b** Experiment scene graph of the first and second protocols: eight (**b1**) and four (**b2**) targets respectively. The scene graph of the third protocol was identical to the first protocol. **c** Hand-cursor relationship in the first phase of the task (*Baseline*): the arrows indicate hand and cursor paths (H and C respectively). **d** Hand-cursor relationship in the last block of the second phase of the task ('b5', *Learning*): 22.5° CCW visuomotor rotation. Screen cursor was rotated by 22.5˚ CCW around the center of the start location.

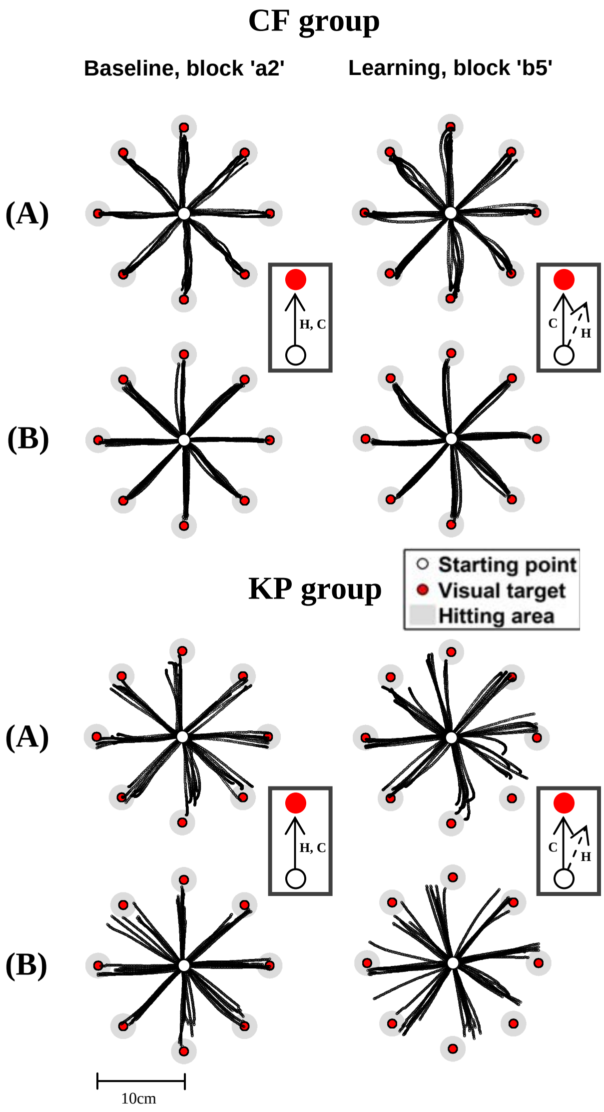


Fig. 2 Cursor paths in the *eight targets protocol*. Cursor paths for the CF and KP groups are shown for the *baseline* (left) and *learning* (right) phases. Grey frames emphasize the hand-cursor relationship in each phase (H and C respectively). **a** Cursor paths of a representative subject. For the baseline phase, the last six cycles of block 'a2' are shown and for the learning phase, the last six cycles of 'b5' are shown**.** For both groups, cursor path longer than 10cm were cut at the 10cm radius. **b** Averaged cursor paths. For each subject, cursor paths for a single target were averaged across the last six cycles. Six subjects per group yielded six mean paths per target. For calculating the mean path, all data points in which there was more than one subject with missing value were eliminated.

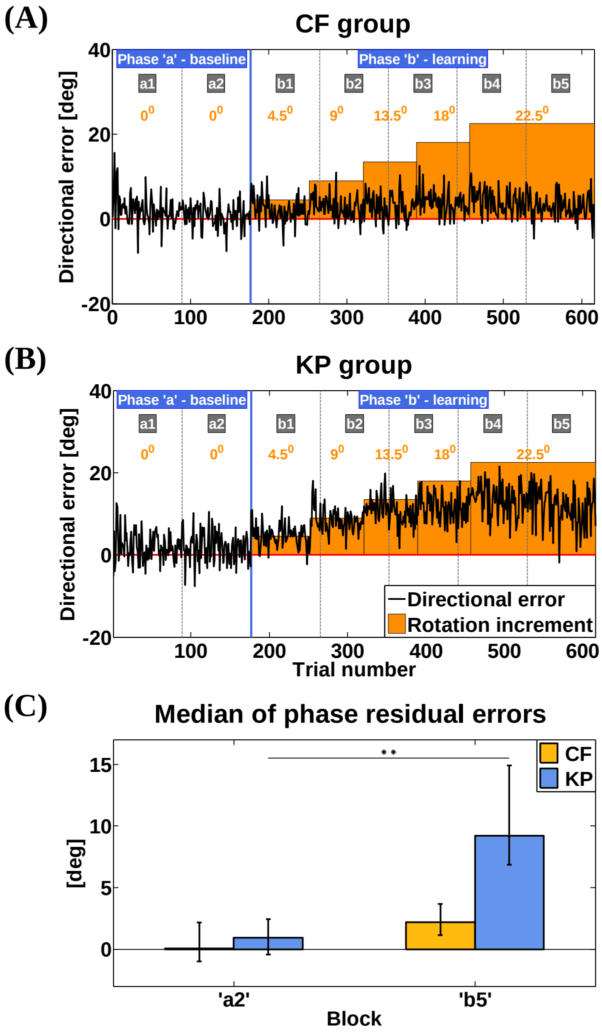
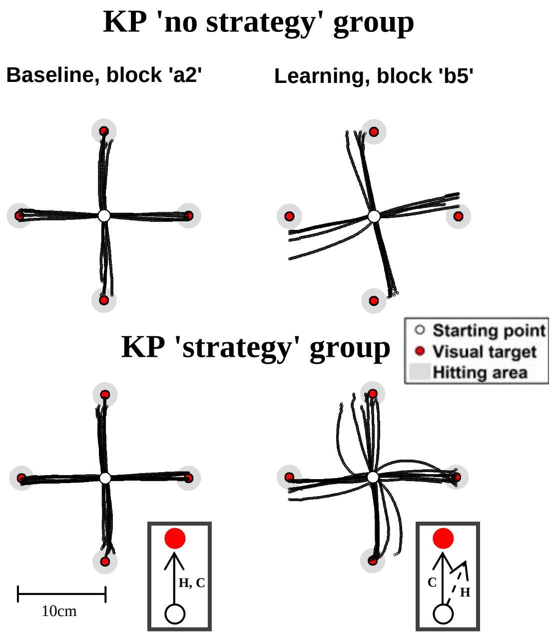


Fig. 3 Adaptation to visuomotor rotation. **a-b** Rotation adaptation curves. Adaptation was estimated by the directional error measured at peak tangential velocity in each trial (see "Data analysis"). Each plot shows group-averaged data along the entire experiment trials. The shaded background and the numeric values on top of it indicate the amount of rotation applied along the experiment progression (see "Experimental paradigm" in "Methods"). **c** Median of the phase residual error (see "Data analysis") with 95% bootstrap CI is shown for the CF and KP groups in blocks 'a2' (*baseline* phase) and 'b5' (*learning* phase). For each subject, the phase residual error was calculated over the last 32 movements of the block and the median was considered separately per block over the subjects of each group. **P<0.01 (ranksum test).



KP 'no strategy' group

Baseline, block 'a2'

Learning, block 'b5'

KP 'strategy' group

Fig. 4 Cursor paths in the *four targets protocol*. Averaged cursor paths of the KP 'no strategy' and 'strategy' groups are shown for *baseline* (left) and *learning* (right) phases, as depicted in figure 2b. For each subject (four 'no strategy' subjects and six 'strategy' subjects), cursor paths for a single target were averaged across the last six cycles. For both groups, cursor path longer than 10cm were cut at the 10cm radius.

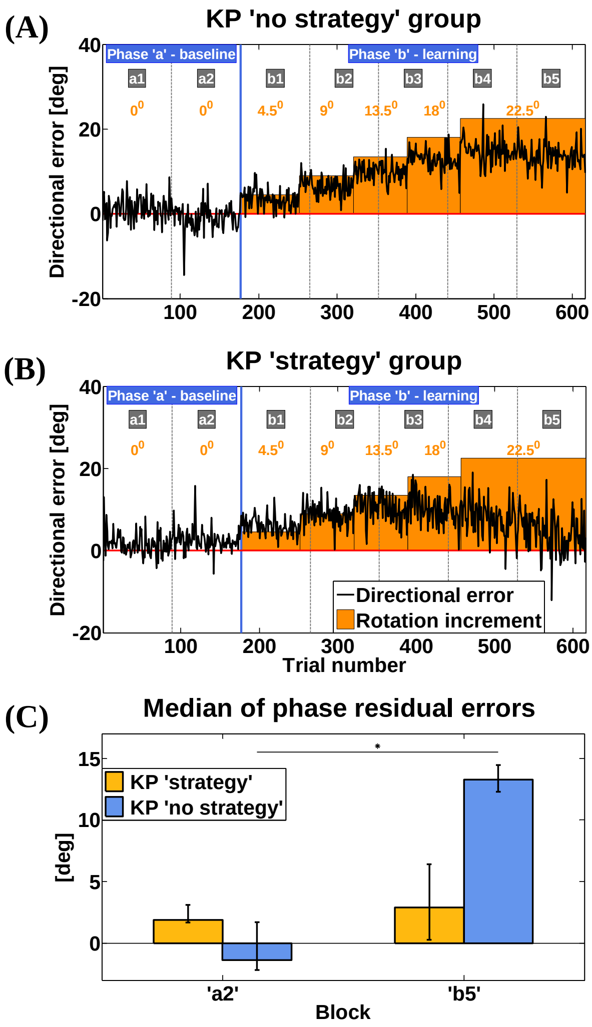


Fig. 5 Adaptation to visuomotor rotation. **a-b** Rotation adaptation curves (see figure 3a and 3b for explanation) for the KP 'no strategy' and 'strategy' groups. **c** Median of the phase residual error with 95% bootstrap CI is shown for the two groups participated in the *four targets protocol* as depicted in figure 3c. For each subject, the phase residual error was calculated over the last 32 movements of the block and the median was considered separately per block over the subjects of the KP 'extended' group. *P<0.05 (ranksum test).

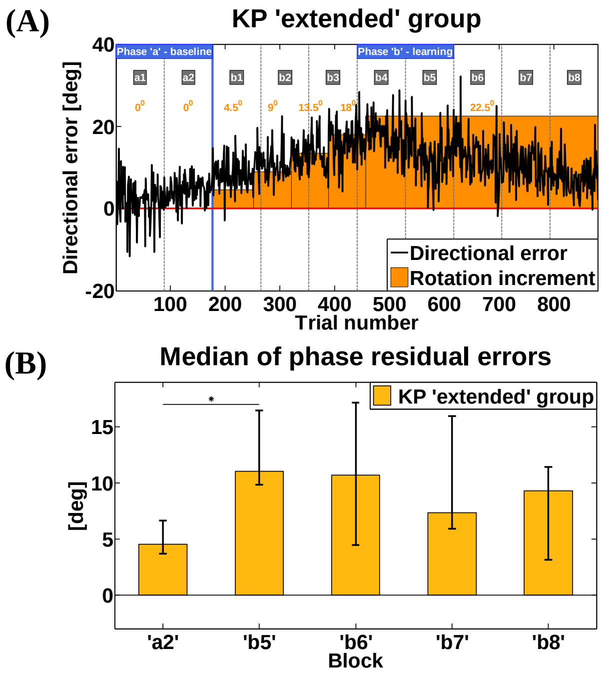


Fig. 6 Adaptation to visuomotor rotation. **a** Rotation adaptation curve (see figure 3a and 3b for explanation) for the KP 'extended' group**. b** Median of the phase directional error with 95% bootstrap CI is shown for the *eight targets extended training protocol* group in blocks 'a2' (*baseline* phase) and 'b5'-'b8' (*learning* phase) as depicted in figure 3c. For each subject, the phase residual error was calculated over the last 32 movements of the block and the median was considered separately per block over the subjects of the KP 'extended' group. *P<0.05 (ranksum test).