Effect of sensory experience on motor learning strategy

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Shou-Han Zhou, Denny Oetomo, Ying Tan, Iven Mareels, Etienne Burdet Sensory information is used in adapting to new environments, but does it determine the strategy used by the central nervous system for this adaptation? To elucidate this question, this study investigates learning of a motor task with different prior sensory experiences. Two groups of subjects learned to execute reaching arm movements in environments with task-irrelevant visual cues, in which all subjects are presented with distorted visual information, namely with velocity dependent error that disappears at the end of each movement. However one group of subjects had a previous experience of learning arm reaching movement using visual cues that are task-relevant. The results demonstrate that the prior sensory experience influences the way in which the new task is learned and executed. The group with no task-relevant visual information experience uses the visual feedback as presented, i.e. they use a motor correction strategy for learning the environment. However it appears that the group that experienced task-relevant visual information uses a motor command that reacts to their estimation of the movement, which involves a more elaborate forward model of the environment, and does not use the visual feedback directly.

Human Motor Learning; Task relevant and irrelevant sensory feedback; Sensorimotor learning strategies

Introduction

Humans have the ability to adapt effectively to visual deformations, as was demonstrated through the use of prismatic glasses (Helmholtz and Southall, 1925; Harris, 1963; Redding and Wallace, 1996; Pisella et al., 2006; Michel et al., 2007). To analyze the visuo-motor learning systematically, recent works have observed modifications of arm reaching when visual feedback is affected during the movement (Flanagan et al., 1999; Krakauer et al., 2000; Scheidt et al., 2005). In this way (Tseng et al., 2007; Sarlegna and Sainburg, 2009; Wei and Kording, 2010; Marko et al., 2012; Schaefer et al., 2012) have emphasized the modification of sensory prediction, while (Wang, 2005) and (Shabbott and Sainburg, 2010) have also showed that visuo-motor adaptation can be explained as the adjustment to a feed-forward controller. In all cases, the mismatch between visual and proprioceptive feedback is compensated based on the amount of error between these two modalities (Wolpert et al., 2011; Richardson et al., 2013; Seidler et al., 2013).

This learning may be related to *visual reflexes* identified in recent works (Day and Lyon, 2000; Saijo et al., 2005; Franklin and Wolpert, 2008; Franklin et al., 2012), i.e. involuntary motor responses opposing visual deformations. Interestingly, these responses are attenuated when the deformation is task-irrelevant, i.e. when it does not prevent the hand from reaching the target for the task of arm reaching (Franklin and Wolpert, 2008). In contrast, visual reflexes persist in task-relevant deformations, and are used to compensate for the observed errors in order to reach the target.

However, the individual effect of these reflexes in human motor learning has so far not been analyzed. Here we study the effect of task- relevant and task-irrelevant errors on the strategy humans use for learning a visual field. In particular, could the learning of task-irrelevant visual environment be affected by training with task-relevant visual feedback? To address this question, two groups of subjects performed reaching movements in a visual environment with a task-irrelevant deformation. However, one group was previously trained in another visual environment producing a task-relevant deformation. The results demonstrate a change of learning strategy caused by exposure to the task-relevant deformations in the visual environment which is systematically analyzed.

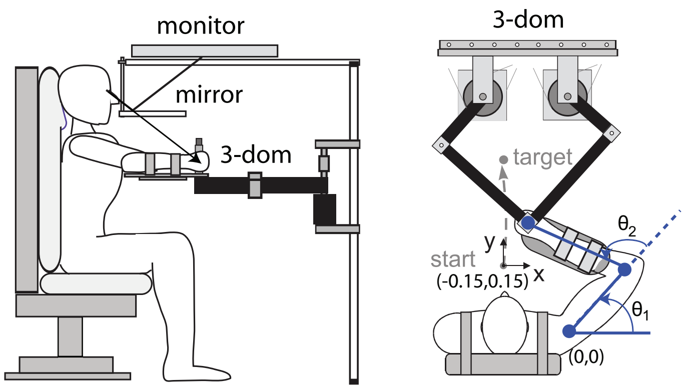

Fig. 1. Setup of the experiment: Subjects perform target reaching movements while their hand is attached to the robot, which supports the arm against gravity and can measure the hand position.

Experiment

Eight right-handed subjects (aged $21-42$, with 4 females) with no reported neurological disorders participated in the experiment as the first group (*G1 group*). A group of six subjects (aged $23-40$, with 3 females) participated as the second group (*G2 group*). The experiments of this study were approved by the Imperial College ethics committee and the subjects gave written consent prior to performing the experiment.

Setup

The apparatus setup for the experiment is shown in Figure 1. The robot is a stiff four-bar linkage offering little resistance to motion, which is equipped with optical encoders to measure the joints angle at $1kHz$. Each human subject is required to sit on a chair while his/her hand is strapped to a cuff attached to the robot end effector, which prevents wrist movement and provides support to the arm against gravity. The subject's arm is therefore restricted to planar movement and can be modeled as a two bar serial linkage.

The hand movement is recorded in Cartesian coordinates $[x^H\, y^H]^T \in \mathbb{R}^2$ relative to the shoulder. The cursor's position $[x^C\, y^C]^T \in \mathbb{R}^2$ on the computer screen is reflected from a

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Contributions

SZ EB DO YT IM developed the concept of the study. SZ EB designed the experiment. SZ performed the experiment. SZ EB DO YT IM conducted the analysis, data interpretation and drafted the manuscript.

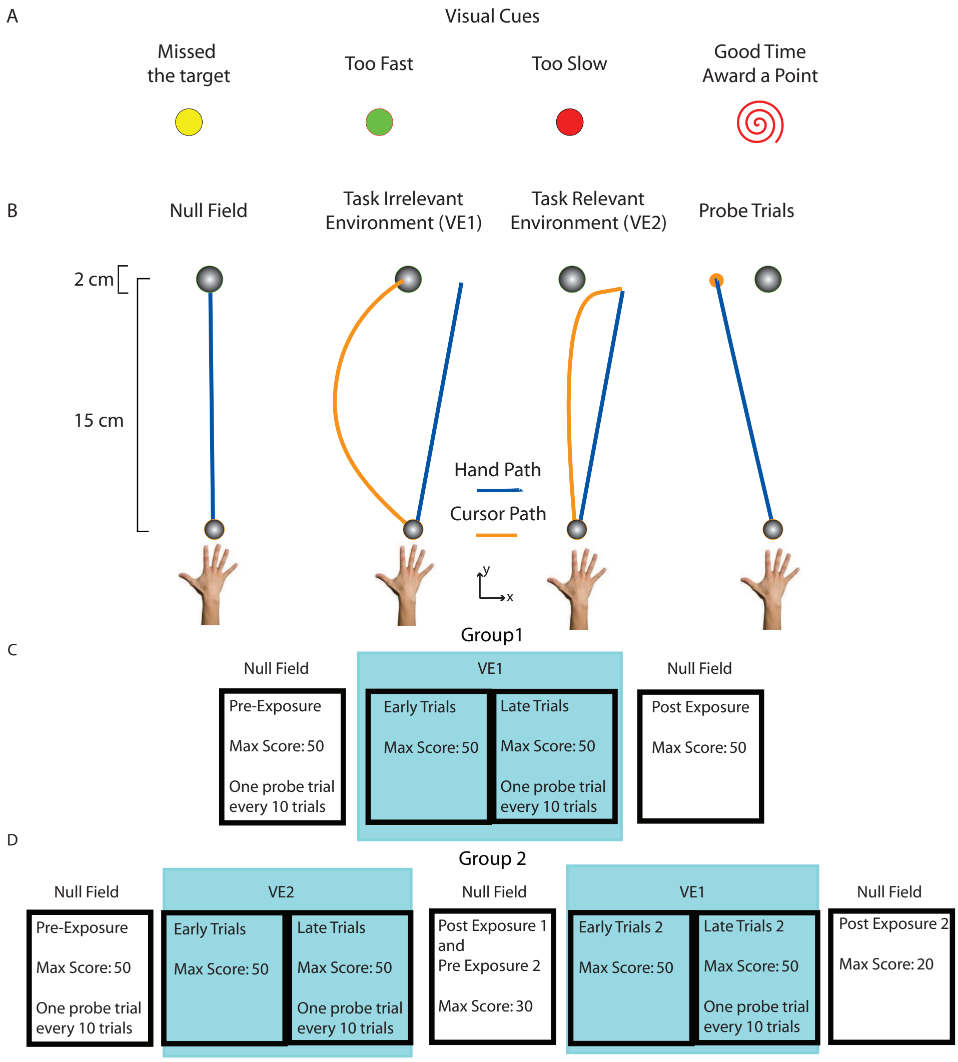

Fig. 2. Experiment protocol.

mirror separating the subject's eyes from the hand, enabling the experimenter to generate any computer-controlled visual distortions by modifying the cursor position from the actual hand position. Both the cursor and the hand movements are recorded at $200Hz$. The start and end of the movement recordings are determined from a velocity threshold of $0.03m/s$ as in (Tseng et al., 2007).

Protocol

The experiment task consisted of performing target reaching movements with the right arm from the start position located at $(-15, 15)cm$ to a $1cm$-radius target $15cm$ away in the y direction. The arm motion is performed on a plane approximately $10cm$ below the subject's shoulder level.

Before each trial, the target and the cursor appear and the robot ceases to apply any force, enabling the subject to perform free movement. After each trial, the cursor disappears and the robot moves the subject's hand back to the starting position for next trial. In this way, no visual feedback is provided to the subject's hand at the end of each movement, preventing him or her from easily noticing the discrepancies between the hand position and the cursor positions (Franklin et al., 2008).

If the hand reaches the target in $700 \pm 100ms$, the target displays a ripple and the movement is rewarded with a point. If the movement is too fast or too slow, there is no reward and the target's color is modified as shown in Figure 2A. The subjects are required to obtain a score of 200 points (*G1 group*) or 300 points (*G2 group*) in order to complete the

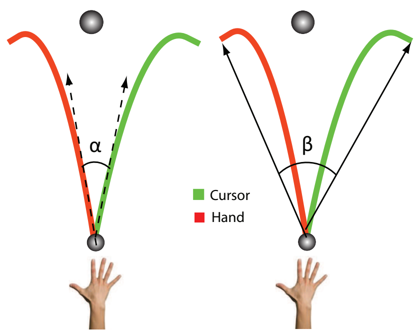

Fig. 3. Definition of angles α and β determining the initial and final movement directions, respectively defined in equations (4) and (5).

experiment. The subjects are informed that their movements may be affected during the experiment.

Two types of *visual environment* are provided to the subjects (Figure 2B). In environment 1 (*VE1*) the cursor position $(x^C\ y^C)^T$ is related to the hand position $(x^H\ y^H)^T$ as

$$\begin{pmatrix} x^C \\ y^C \end{pmatrix} = \begin{pmatrix} 0.1\dot{y}^H \\ y^H \end{pmatrix} \quad [1]$$

where $\dot{y}^H$ represents the hand's velocity in the y-direction. Note that when the subjects stop moving, $\dot{y}^H \equiv 0$ and the cursor does not induce any end-point error in the x-direction. In environment 2 (*VE2*)

$$\begin{pmatrix} x^C \\ y^C \end{pmatrix} = \begin{pmatrix} x^H + 0.1\dot{y}^H \\ y^H \end{pmatrix} \quad [2]$$

When the subjects finish the movement in this environment, $\dot{y}^H \equiv 0$ and the realized cursor position is aligned with the subject's hand position. Therefore deviations of the hand from the target are reflected on the screen and the subjects need to correct for this error, which is in contrast to the first environment (VE1).

Probe trials are used to observe changes in the planned movement. In these trials, the visual cursor is turned off, so that subjects have no visual feedback during movement, but can see their final hand position after they have completed the movement.

The subjects in G1 group perform arm reaching movements in VE1 according to the protocol given in Figure 2C. In a form of primitive reward, subjects progress through different phases of the experiment by completing a given number of *successful trials* (Figure 2C, D), i.e., trials reaching the target in the suitable duration. The *starting phase* consists of trials without visual deformation, during which the subjects can experience the task and the robot dynamics. After fifty successful trials, VE1 is switched on to the *unsuspecting* subject, who has been only informed that changes may occur during the experiment but not the form of the changes nor when the changes would takes place. In the subsequent *learning phase*, the subjects carry out the trials until they have produced 50 successful trials. This is followed by a *learned phase* with a 50 successful trials target during which probe trials are randomly integrated. Finally, a *washout phase* is applied with a target of 20 successful trials in which the environment is turned off. Any effects from the environment can be observed by comparing the post-null field probe trials of the washout phase with the pre-null field probe trials of the starting phase.

The subjects in G2 group are required to perform arm reaching movements in VE2 before completing movements in the VE1 (Figure 2D). VE2 is learned with the same protocol as above, and the subsequent learning of VE1 follows directly the phase of post exposure. That is, the post exposure phase is used both to observe the learning of VE2 and to initialized for the subsequent learning under VE1.

Data Analysis

The data of the hand position is collected during the experiment. The hand velocity is computed using numerical differentiation followed by a fifth order zero phase Butterworth low pass filter with a cut-off frequency of 30Hz. Three measures are used to analyze learning:

1. The *absolute hand path error* of each trial is defined as the area delimited by the hand path and the cursor path (Burdet et al., 2001):

$$S = \sum_{i=1}^{\mathcal{N}} \left| x^H(i) - x^C(i) \right| \left| \dot{y}^H(i) \right| \quad [3]$$

where $\mathcal{N}$ is the total number of points collected during the trial.

2. The *initial direction error* α depicted in Figure 3 is calculated as the difference between the velocity vectors of the hand and the cursor over the first quarter of the trajectory:

$$\alpha_k = \arctan\left(\frac{\Delta(\dot{y}^H_{int}, \dot{y}^H_0)}{\Delta(\dot{x}^H_{int}, \dot{x}^H_0)}\right) - \arctan\left(\frac{\Delta(\dot{y}^C_{int}, \dot{y}^C_0)}{\Delta(\dot{x}^C_{int}, \dot{x}^C_0)}\right) \quad [4]$$

where $x_{int} = x(\mathcal{N}/4)$ and $\Delta(r,s) = r - s$.

3. The *final direction error* β depicted in Figure 3 is defined as the difference between the directions of the positions of the hand and cursor at the end of their movement, relative to the movement start position:

$$\beta_k = \arctan\left(\frac{\Delta(y^H_f, y^H_0)}{\Delta(x^H_f, x^H_0)}\right) - \arctan\left(\frac{\Delta(y^C_f, y^C_0)}{\Delta(x^C_f, x^C_0)}\right) \quad [5]$$

All trials are considered in the results analysis, and the trials in each phase are normalized so that the performances of different subjects can be compared (e.g. in Figures 6 and 8).

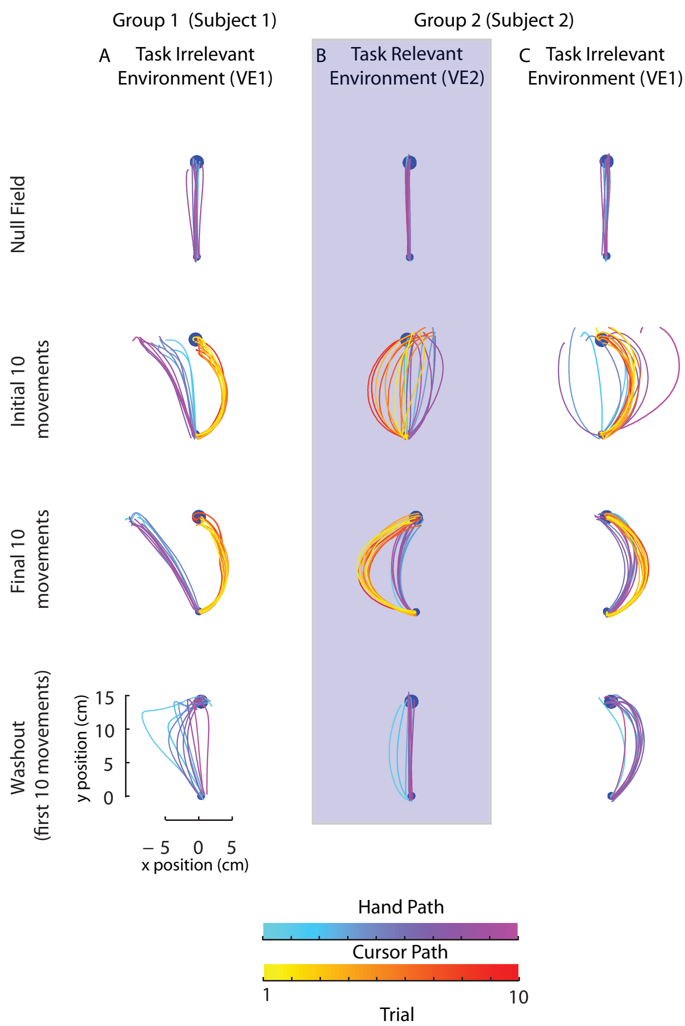

Fig. 4. Evolution of cursor trajectories (solid yellow to red lines) and hand path (solid blue to purple lines) for two representative subjects of group 1 and group 2. Observe the different effect of VE1 and VE2 in the two first columns, as well as the effect of previous learning of VE2 on the learning in VE1 by comparing the first and third columns. Because the cursor is aligned with the hand in the null and washout fields, only the hand paths is plotted.

Results

In this section, the results of typical subjects of each group are first described and then systematically analyzed to identify the relevant learning patterns.

Qualitative evolution of movement paths and direction

In the Null Field, the hand paths made by *subject 1* of group 1 and by *subject 2* of group 2 resemble a straight line (Figure 4, Null Field row).

In the task-relevant environment VE2, subject 2 initially moves in the opposite direction to the deformation (Figure 4B, First 10 Movements), before learning to move in the same direction as the cursor movement (Figure 4B, final 10 Movements). When the visual deformation of VE2 is turned off, the subject quickly reverts to the straight-line trajectory (Figure 4B, Washout).

In the task-irrelevant environment VE1, it is seen that subject 1's hand immediately deviates from the straight line trajectory (Figure 4A, First 10 Movements). The hand path continues to drift with consecutive trials in the opposite direction to the deformation (Figure 4A, Last 10 Movements).

In the same environment, subject 2's hand path moves away from the visual deformation on the very first trials (Figure 4C, First 10 Movements). However, unlike the results observed with subject 1 in Figure 4A, subject 2 learns to follow the observed deformation in this environment. After sufficiently many trials in VE1, the subject settles to following the visual cursor, resulting in the hand reaching the actual target (Figure 4C, Last 10 Movements).

In the washout trials of VE1, significant adjustments are made by subject 1, with the subject returning to the straight line trajectory (Figure 4A, Washout). However, the washout trials of subject 2 in VE1 are not adjusted and continue to move along a curved line (Figure 4C, Washout).

To further analyze the evolution of movement of subjects 1 and 2, we use the absolute hand path error, the initial direction error and final direction error between hand and cursor trajectories defined in the Methods.

In VE2 (Figure 6A, C, E), the cursor deviates from subject 2's hand, creating an arc, as reflected by the change of hand path error (Figure 6A). Subject 2 maintains the movement in subsequent trials and consequently no significant change is observed between the cursor and the hand. This suggests that the subject attempts to maintain a straight line trajectory in VE2, as reflected in Figure 4B.

In Figure 6C, the initial angle is observed to deviate immediately when VE2 is introduced while in Figure 6E, the final angle is observed to not change across all four phases. This suggests that the subject moves in a similar trajectory as if he/she was moving without the visual deformation while using online correction to adjust for the environment change. Therefore, Figure 6C implies that the subject's feed-forward commands is not altered in the environment while Figure 6E shows that the subject modifies the feedback command to compensate for the visual environment.

In VE1 (Figure 6B, D, F, subject 2), subject 2 persists with the same strategy over the trials, keeping the hand at a certain distance from the cursor. Interestingly, the hand path error in VE1 is less than in VE2, indicating that the subject has improved performance in VE1 as a consequence of training in VE2. It is observed in Figure 4C that this improvement is a consequence of the subject following the cursor instead of maintaining a straight line.

This behavior contrasts with subject 1's performance in VE1 (Figure 6B, D, F, subject 1) whose movement is observed to drift away from the cursor. This difference between the cursor trajectory and the actual hand trajectory results in the subject's hand not reaching the target (Figure 6F, subject 1). However, in this task-irrelevant environment, the subject is still able to bring the cursor to the target in VE1 and complete the task.

Quantitative analysis

The bar plots of Figure 5 and associated t-test at 5% significance level are used to examine whether the differences in behavior between subjects from the two groups observed in VE1 are valid for their whole group.

For group 1, all three measures of hand path error, initial direction angle and final error angle *increased* during the

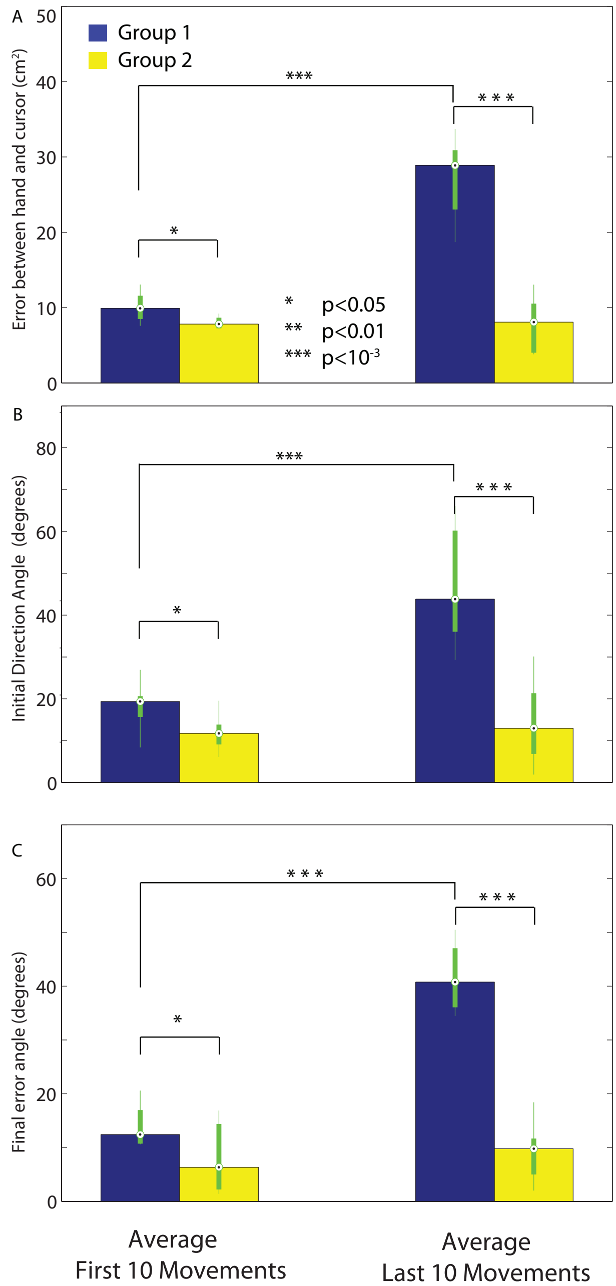

Fig. 5. Comparison of learning performances during the first and last 10 movements made by the two groups in visual environment VE1. The black start '*' indicates significance level over all subjects.

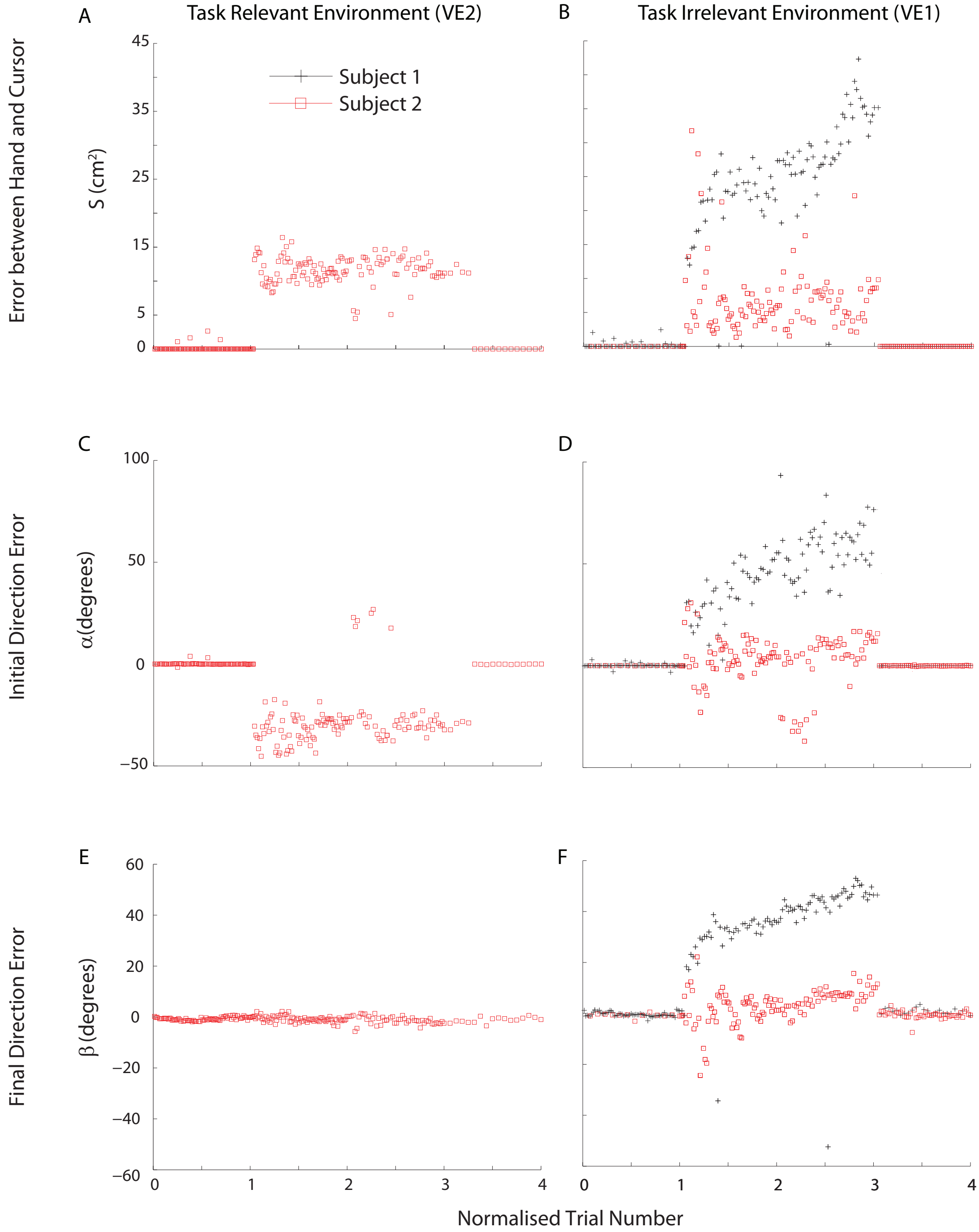

Fig. 6. Analysis of hand path error (panels A, B) and direction error (panels C-F) in the two visual environments.

last 10 movements in VE1 compared to first 10 movements in VE1 ($p < 1e^{-4}$ for all subjects). This means that subjects in this group drift away from the cursor as they learn the environment.

For group 2, all three measures indicate that there is little change between the subjects' first and last 10 movements in VE1 ($p > 0.17$ for each subject). In addition, the measures of group 2 are always smaller than that of group 1 ($p < 0.05$ for the first 10 movements of all subjects and $p < 1e^{-3}$ for the last 10 movements of all subjects). This implies that the subjects in group 2 are not as sensitive to the environment VE1 as the subjects in group 1. More importantly, the difference in the three measures for the last 10 movements of the two groups in VE1 indicates that they are learning a different trajectory to achieve the task. This final trajectory is consistent among subjects within each group but not between the two groups.

In the washout trials, the two groups exhibit distinctly different behavior as shown in Figure 7. In this figure, the three measures involve the difference between the hand path of each trial and the straight line (not between the hand and the cursor as before). It is seen that the subjects in group 1 have a higher error and initial angle magnitude compared to the subjects in group 2 (Figure 7A, B, $p < 0.01$ for all subjects). The two groups have similar final direction error (Figure 7C, $p > 0.7$ for all subjects) not significantly different from zero ($p > 0.3$ over all subjects). For group 2, the initial direction error is also not significantly different from zero ($p > 0.5$ for all subjects). Considering that the visual environment was the same in both groups, this suggest that subjects of group 1 attempt to move to the other direction of the visual field and the movement is significantly corrected online, compared to subjects of group 2 who try to move along a significantly straighter trajectory.

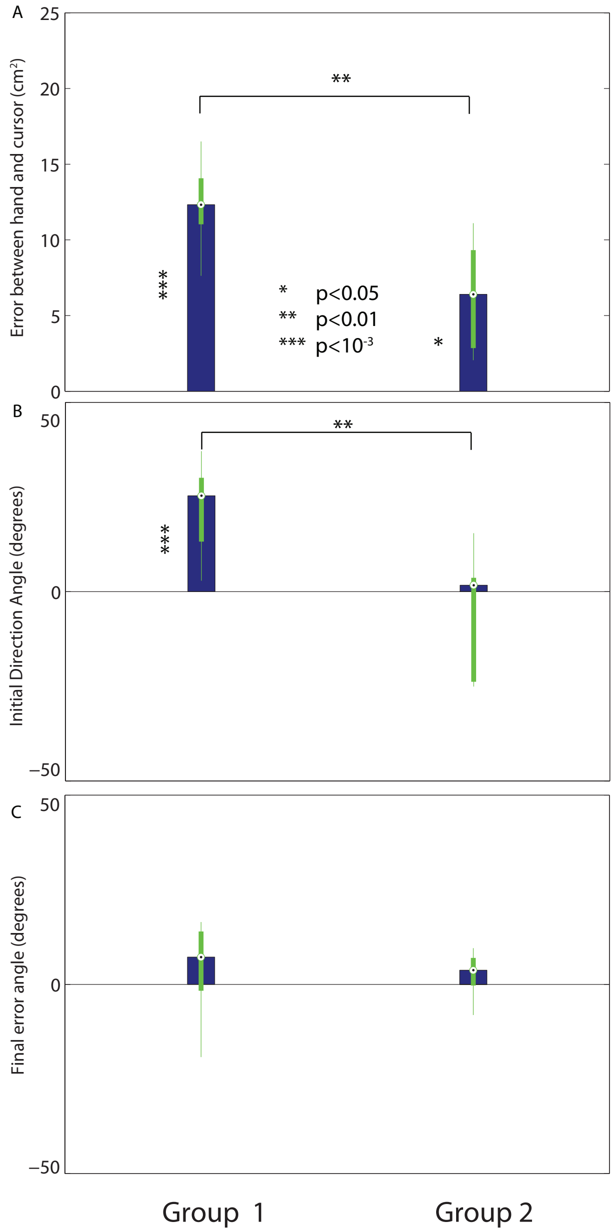

Fig. 7. Comparison of learning performances in the washout trials made by the two groups in visual environment VE1. The black star '*' indicate significance level over all subjects. The vertical black stars represent the significance of the data from a population with a mean of zero.

Discussion

This study examined how training with task-relevant feedback affects the behavior in learning of task-irrelevant environment. Two groups of subjects learned target reaching movements in task-irrelevant environment VE1 while group 2 had previously trained in task-relevant environment VE2.

In the task-irrelevant environment VE1, subjects from group 1 moved in the opposite direction to the lateral visual deformation as observed in previous works (Flash, 1987; Latash et al., 1999; Feldman and Latash, 2005; Franklin et al., 2008, 2012), possibly due their visual reflexes. Over trials, the subjects drifted further away from the target. Such drifting was also observed when visual feedback was not available during the movement (Brown et al., 2003; Salaün et al., 2009). According to the study reported in (Tseng et al., 2007), this would correspond to a "motor correction" using the error between the cursor and the straight line to adjust motor commands across trials. In VE1, this strategy does not decrease the task-irrelevant errors, but accumulates them in the motor commands, resulting in the drift that prevented the cursor from reaching the target.

Humans prioritize errors

When subjects of group 2 use the same strategy to correct for the task-irrelevant errors in VE2, the endpoint cursor deviates from the target. Therefore, they use visual reflexes and voluntary visual corrections to adjust the movement online and ensure that the hand reaches the target. Over trials, these subjects learn to ignore the task-irrelevant errors and maintain a relatively straight trajectory in order to perform the task, as was observed in (Franklin and Wolpert, 2008). In this light, reaching the target is higher priority (the primary task) than correcting task-irrelevant errors (the secondary task), which is ignored if it conflicts with the primary task.

Sensory prediction strategy

Although the subjects from group 2 ignore the task-irrelevant errors in VE2, they tend to subsequently follow the cursor in VE1. Furthermore, they maintain a low initial direction error for all trials. Considering that changes in initial direction angle is associated with adjustment of human's feed-forward commands (Wang, 2005; Sarlegna and Sainburg, 2007; Scheidt and Ghez, 2007; Shabbott and Sainburg, 2010), this suggests that the subjects learn to minimise the difference between the cursor and the hand trajectory. This corresponds to adjusting sensory prediction, the difference between the observed states (vision) and the predicted states (hand), across trials (Wolpert et al., 1995; Miall and Wolpert, 1996; Tseng et al., 2007; Shadmehr et al., 2010; Wolpert et al., 2011; Schaefer et al., 2012). This strategy results in an internal forward model of the environment, enabling the subjects to compensate for the deformations in VE1.

Note that it is possible that the same strategy was also employed by group 2's subjects in VE2. However, due to the presence of task-relevant error, such strategy was considered as a secondary task and consequently had less influence on the subject's movement. A closer observation in Figure 4B shows that the initial angle made by subject 2 in the last 10 movements of VE2 is significantly different from the corresponding final angle ($p < 0.003$). This would not have been the case if subjects had learned to ignore the task-irrelevant errors.

Control strategies are affected by previous experience

The different strategies employed by subjects of groups 1 and 2 in VE1 suggest that task-relevant errors can affect the strategy used by a subject for learning and for maintaining movements in visual fields (Figures 5 and 7).

Previous investigations have found that human subjects change their reliance on feed-forward or feedback information for learning and for motion depending on their previous experiences (Kagerer et al., 1997; Saijo and Gomi, 2012). The current results show that experience can also change the *strategy* which humans use for learning. In particular, subjects use different learning strategies depending on whether they have previously been trained in environments involving task-relevant errors.

The findings can explain the absence of the learning behaviour of group 1 for visual-related experiments in the literature (Krakauer et al., 2000; Baraduc et al., 2001; Mistry and Contreras-Vidal, 2004; Scheidt et al., 2005; Izawa et al., 2008; Wolpert et al., 2011). Current visual experiments involve environments containing task relevant visual errors, triggering the CNS to use modification of sensory prediction for learning. This may explain why such experiments emphasised forward models to interpret human motion in visual environments (Wolpert et al., 2003; Izawa et al., 2008; Krakauer and Mazzoni, 2011).

Modification of reliance on estimation and vision

The observed behaviour in the experiments exhibits how task-relevant errors affect human's strategy in learning and in motion control. A plausible explanation is that the strategy change is a result of the subject changing their reliance on sensory feedback. This is motivated by the different strategies employed by two groups in VE1. Spontaneously, the subjects from group 1 would rely mainly on vision to correct for perceived error. This is evidenced in Figures 4A and 5 in which subjects learn to move to the opposite direction to the cursor movement. On the other hand the subjects who had previous training in task relevant environment seem to rely mostly on an estimation of motion obtained from an efferent copy of the motor command, as evident from subjects learning to move in the same direction as the cursor (Figures 4C and 6).

It is possible that during training in VE2, subjects become aware that their vision is not sufficient, and consequently use estimation to control their arm instead, resulting in the changes in strategies. While modifications of reliance on vision and estimation relative to the knowledge of the sensor noise distribution has been observed previously in human motor control under the Bayesian framework (Ernst and Banks, 2002; Körding and Wolpert, 2004), here it is observed how previous experience has a decisive effect on learning. In particular, the results show how task-relevant errors modify the reliance between vision and estimation, which in turn determines the strategy employed for learning.

Roles of vision and estimation

In the experiment, subjects from group 2 use in the task-irrelevant environment a control strategy relying on estimation, and are able to succeed with the strategy in learning to perform movements in both task relevant environment VE1 and in task irrelevant environment VE2. If so, why do humans usually rely mainly on vision for their learning of novel environments (i.e. group 1's strategy in VE1)?

Under the Bayesian framework (Körding and Wolpert, 2004, 2006; Wolpert et al., 2011), humans tend to use feedback with the least amount of noise. A possible explanation is therefore that humans use vision for moving and learning because it generally has less uncertainty compared to estimation. This is evident in that vision is necessary for movement calibration to ensure that human movement starts and finishes at suitable locations (Brown et al., 2003).

On the other hand, reliance on vision results in task-relevant errors in visual environments such as VE2. It is possible that the task-relevant errors decrease the human's trust in visual feedback, resulting in the human relying more on estimation of motion from an efferent copy of the motor command as the main source of feedback for motor control and learning.

An alternative or complementary explanation is that the use of vision for motor corrections presents a more simple method of learning compared to using estimations. This is because the latter strategy incorporates an internal model of the environment in the forward model, which is not required in the former strategy. Therefore, it appears that humans use an occam's razor approach for learning (MacKay, 2003): they do not attempt to learn the environment unless it is necessary to perform the task, since such learning requires more cognitive effort than learning using motor corrections through visual reflexes.

Current computational frameworks (Wolpert et al., 2003; Franklin et al., 2008; Haith et al., 2009; Zhou et al., 2012)

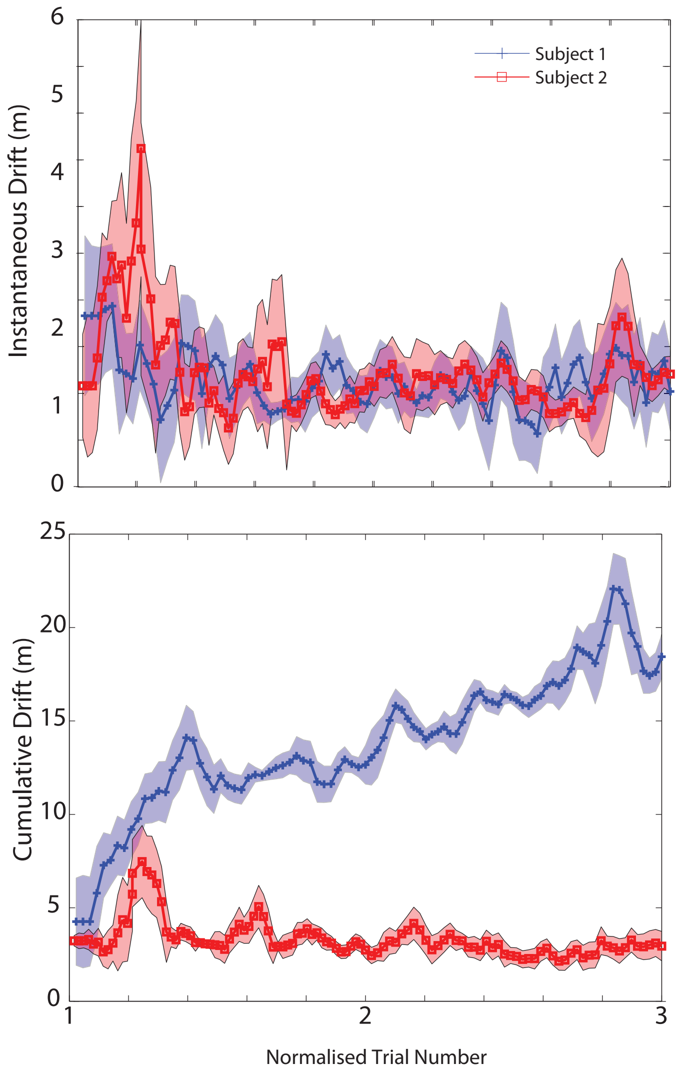

Fig. 8. Drift of the final position of the current trial relative to the final position of the previous trial (Instantaneous Drift) and to the final position of the first trial (Cumulative Drift) for the two subjects when they repeat reaching movements in the task-irrelevant visual environment VE1.

presents a single controller scheme to model human motor learning. They do not consider human's ability to change their learning strategies according to their prior sensory experiences. Such ability needs to be considered in order to yield a more accurate model of human motor learning.

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