Effect of sensory experience on motor learning strategy

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Introduction

Humans have the ability to learn with visual deformations effectively, 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 systematically analyze visuo-motor coordination learning, recent works have observed modifications to arm reaching movements when visual feedback is affected during the movement (Flanagan et al., 1999; Krakauer et al., 2000; Scheidt et al., 2005). This learning was interpreted by processes involving sensory prediction (Tseng et al., 2007; Sarlegna and Wolpert, 2008; van Beers et al., 2013).

While the works discussed above show how the mismatch of hand and visual target are reduced by learning, this paper investigates whether this mismatch can affect the learning strategy itself. The above learning strategies/processes may rely on visual reflexes as proposed 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 the mismatch between the hand and the visual cursor. Interestingly, these visual reflexes can be inhibited by the CNS in carefully designed environments (Franklin and Wolpert, 2008). Therefore, could the choice of a strategy, e.g. gradual adaptation of planned movement or switching between distinct planned movements, be affected by the type of visual environment provided? To address this question, we designed an experiment in which two groups of subjects performed reaching movements in a visual environment with a task-irrelevant deformation, where one group was previously trained in another visual environment producing a task-relevant deformation. We analyzed the resulting behavior and adaptation. The results demonstrate that the task-relevant errors affect the subjects’ learning strategy, yielding different learning behaviors.

Experiment

Eight right-handed subjects (aged 21 – 42, with 4 females) with no reported neurological disorders participated in the study 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 study was 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. It is equipped with optical encoders to measure the joints angle at a sampling rate of 1 kHz. 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 any wrist movement and provides support to the arm against gravity. The subject’s arm is therefore restricted to planar movements and can be modeled as a two bar serial linkage with revolute joints at the end of each link. To prevent movement of the upper body, each subject is required to rest against a head-rest which is fixed onto the robot frame.

The hand movement is recorded in Cartesian coordinates \([x^H, y^H, z^H] \in \mathbb{R}^3\) relative to the shoulder. The cursor position \([x^C, y^C, z^C] \in \mathbb{R}^3\) on the computer screen is reflected from a mirror which removes the subject’s hand from his/her field of vision, 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 200 Hz.

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

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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 the next trial. In this way, no visual feedback is provided to the subject at the end of each movement, preventing him or her from easily noticing the discrepancies between the hand and the cursor positions (Franklin et al., 2008).

If the hand reaches the target in 700 ± 100 ms, the target displays a ripple and the movement is rewarded with one point, as shown in Figure 2A. If the movement is too fast or too slow, there is no reward and the target’s color is modified accordingly (Figure 2A). The subjects are required to obtain a score of 100 points (G1 group) or 180 points (G2 group) in order to complete the experiment. The subjects are informed that their movements may be affected during the experiment.

Two types of visual environments are provided to the subjects (Figure 2B). In environment 1 (VE1) the cursor position \((x^C_0, y^C_0)^T\) is related to the hand position \((x^H, y^H)^T\) as

\[
\begin{align*}
(x^C_0, y^C_0)^T &= \left( x^H + 0.1 y^H, y^H \right)^T 
\end{align*}
\]

where \(y^H\) represents the hand’s velocity in the \(y\) direction and \(x^C(0) = x^H(0)\) is the starting cursor position in the \(x\) direction. Under this environment, the cursor and the hand start at the same position. When the subject begins to move towards the target, the cursor deviates from the subject’s hand trajectory in the \(x\) direction proportionally to the speed of the hand movement in the \(y\) direction. At the end of the trial, the subject’s hand stops moving and the cursor settles on the line joining the centers of the starting point and the target. Therefore, there is no error between the cursor’s final position and the target in the \(x\) direction, i.e. this environment does not induce any end-point error in the \(x\) direction.

In environment 2 (VE2) is implemented as

\[
\begin{align*}
(x^C, y^C)^T &= \left( x^H + 0.1 y^H, y^H \right) 
\end{align*}
\]

In this environment, the cursor deviates from the hand as the subject reaches for the target. The cursor then settles at the subject’s hand at the end of the trial when the subject’s hand stops moving. In this environment, deviations of the hand from the target are therefore reflected on the screen which the subject is required to minimize. This 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 the movement, but can see the position reached by their hand position when they have completed the movement.

Before the experiment, the subjects are informed that changes will occur during the experiment but are not informed of the form of the changes nor when the changes would take place. The subjects of both groups progress through different phases of the experiment according to the protocols given in Figures 2C and 2D, respectively. As a simple reward, the subjects progress through different phases of the experiment by completing a given number of successful trials i.e. trials in which the target is reached in the suitable duration.

This way, the subjects are required to have fully learned to perform the task in the given environment before they can progress to the next phase.

The subjects in the G1 group perform the arm reaching movements in VE1 according to the protocol given in Figure 2C. The starting phase consists of trials without visual deformation, during which the subjects can experience the task and the robot dynamics. After 30 successful trials, VE1 is activated for the unsuspecting subject. In the subsequent learning phase, the subjects carry out the trials until they have produced 25 successful trials. This is followed by a learned phase with a 25 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. Learning effects can be observed by comparing the trials of the washout phase with the trials of the starting phase.

The subjects in the G2 group are required to perform arm reaching movements in VE2 before completing movements in VE1 (Figure 2D). The subjects of the G2 group are required to learn VE2 with the same protocol as the subjects of the G1 group. The subsequent learning of VE1 occurs immediately after the washout phase of VE2. The washout phase of VE1 is therefore used to observe the learning of VE2 and is also used as the starting phase for the subsequent learning of 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 30 Hz cut-off frequency. To filter out any movement due to motor noise, the start and the end of the recorded movement are determined from a velocity threshold of 0.03 m/s as in (Tseng et al., 2007). Any movement below this threshold is removed, enabling a comprehensive analysis of the subjects’ movement.

Four measures are used to analyze learning:

1. The absolute hand path area and the absolute cursor path area of each trial are defined as the area delimited by the hand path (Burdet et al., 2001), as shown in Figure 3A:

\[
S^H = \sum_{i=1}^{N} \left| x^H(i) - x^H(0) \right| \left| y^H(i) \right| 
\]

\[
S^C = \sum_{i=1}^{N} \left| x^C(i) - x^C(0) \right| \left| y^C(i) \right| 
\]

where \(N\) is the total number of points collected during the trial.

2. The hand initial direction \(\alpha^H\) and the cursor initial direction \(\alpha^C\) are computed as the direction of the hand and the cursor for the first quarter of the trajectory (Figure 3B)

\[
\alpha^H = \arctan \left( \frac{y^H(N/4) - y^H(0)}{x^H(N/4) - x^H(0)} \right) 
\]

\[
\alpha^C = \arctan \left( \frac{y^C(N/4) - y^C(0)}{x^C(N/4) - x^C(0)} \right) 
\]

With this definition, the cursor is always in the negative direction while a positive hand direction indicates that the hand is moving away from the cursor and a negative hand direction indicates that it is moving towards the cursor.

3. Similarly, the hand final direction \(\hat{y}^H\) and the cursor final direction \(\hat{y}^C\) are defined as the directions of the hand and cursor positions at the end of the movement relative to the starting point, \((x^H(0), y^H(0))\) and \((x^C(0), y^C(0))\) respectively.
the start position (Figure 3C)

\[ \beta_k^C = \arctan \left( \frac{y^C(N) - y^C(0)}{x^C(N) - x^C(0)} \right) \]

\[ \beta_k^C = -|\beta_k^C| \]

\[ \beta_k^H = \arctan \left( \frac{y^H(N) - y^H(0)}{x^H(N) - x^H(0)} \right) \]

\[ \beta_k^H = -|\text{sign}(\beta_k^C)\beta_k^H| \]

4. Finally, the difference between the absolute hand-path error and the absolute cursor error is defined as

\[ S^E = S^H - S^C \]

where \( S^H \) and \( S^C \) are the absolute hand and cursor error defined in (3) and (4) respectively.

All trials are considered in the results analysis. In order to compare the performances between different subjects, a spline is first fit to the data of each subject across trials. This spline is then used to interpolate between trials in order to generate 200 trials per phase.

Results

The results of typical subjects in each group are first described and then systematically analyzed to identify the relevant learning patterns.

Evolution of hand and cursor movement paths. The subjects of the G2 group performed more trials than that of the G1 group (a mean of 274 for the G1 group and 388 for the G2 group). However, the two groups have large standard deviations (std = 140 for the G1 group and std = 123 for the G2 group). To compare the results of the two groups, the movements of one representative subject of each group are shown in Figure 4. The subjects performed a similar number of trials (364 and 387 trials, respectively).

In the Null Field, the hand paths made by subject 1 of the G1 group and by subject 2 of the G2 group join the starting point and the target in approximately 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, Initial 10 Movements), before learning to move in the same direction as the cursor movement (Figure 4B, Final 10 Movements). This behavior is maintained in the probe trials (Figure 4B, Probe Trial). 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, subject 1's hand immediately deviates from the straight-line trajectory (Figure 4A, Initial 10 Movements). The hand path continues to drift with consecutive trials in the opposite direction to the visual deformation (Figure 4A, Final 10 Movements). This behavior is not modified in the probe trials, during which the subjects made the same movements as observed when the visual field was turned on (Figure 4A, Probe Trials).

In the same environment VE1, subject 2's hand path moves away from the visual deformation on the very first trials (Figure 4C, Initial 10 Movements). However, unlike the results of subject 1 in Figure 4A, subject 2 settles on moving along the same curve as the visual cursor after sufficiently many trials, similar to his/her movements in the VE2 environment (Figure 4C, Final 10 Movements). The subject maintains the curved movement in the probe trials, resulting in the hand reaching the actual target (Figure 4C, Probe Trials).

In the washout 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 the subject continues to move along the curved path (Figure 4C, Washout).

Population behavior. To examine whether the results of subjects 1 and 2 can be generalized across the population, the mean and standard deviation of the first six measures (3)-(8) defined in the Data Analysis section (i.e. the absolute hand path area, the hand and cursor initial directions and the hand and cursor final directions) are plotted against the normalized trials for groups G1 and G2 in Figure 5A. The bar plots of Figure 5B and Figure 5C and the associated t-tests are used to examine the significance of the behaviors observed between the two groups.

In VE2, the hand of the G2 group moves away from the straight line toward the cursor (Figure 5A.4). The subjects consistently maintain their path with similar curvature in the subsequent trials during learning. Furthermore, their hand path drifts towards the cursor direction as they learn the field while their final hand position is maintained at the target (Figure 5A.5, A.6). This behavior is reflected in the movements of subject 2 in Figure 4B.

In VE1, the G2 group subjects move in the same direction as the cursor, as they have done previously in VE2 (Figure 5A.7-A.9). This behavior persists until the last few trials, where the G2 group's initial direction begins to move towards the straight line (Figure 5A.8), while the final direction drifts slightly away from the cursor trajectory (Figure 5A.9). The G2 group eventually returns to the straight line trajectory in the washout trials (Figure 5A.7-A.9).

Compared to the respective behaviors in VE2, the performance of the G2 group in VE1 possesses similar hand path area as seen in Figure 5B (p > 0.65 for early learning and p > 0.39 for late learning). Furthermore, the subjects learn similar trajectories in the two environments, with similar initial and final directions during late learning (p > 0.2 for initial direction and p > 0.3 for final direction). There exists little change in the performance measures during the probe trials during which the cursor position is removed (Figure 5C, p > 0.6, p > 0.73, p > 0.5 for the three measures respectively), suggesting that the learning occurs in a feed-forward manner.

In VE1, the G1 group is observed to move away from the straight line in the direction opposite to the cursor (Figure 5A.1-A.3). The G1 group's initial direction increases in the direction opposite of the cursor and the direction is maintained throughout the trials (Figure 5A.2). Similarly, the G1 group's final direction moves away from the straight line in the environment, resulting in the subject's hand failing to reach the target (Figure 5A.3, hand). In this task-irrelevant environment, the G1 group is still able to bring the cursor to the target and complete the task (Figure 5A.3, cursor).

In the washout trials, the G1 group's movements return to the straight line. The fast decrease of the final direction (Figure 5A.3) compared to the slow decrease of the initial direction (Figure 5A.2) is reflected in subject 1's movements in the field VE1 (Figure 4A).

Compared to the G2 group's behavior in VE1, the G1 group demonstrated similar hand path area and final direction for early learning (Figure 5B, p > 0.3 and p > 0.05 respectively). However, in late learning, significant changes are observed between the two groups (p < 0.01 and p < 1e−5).
for hand path area and final direction, respectively). The hand initial directions of the two groups in the field are consistently different across trials ($p < 0.01$ for early learning and $p < 1e-5$ for late learning).

Similar to the G2 group, the movement of the G1 group is of feed-forward nature, resulting in insignificant change in the behavior during the probe trials (Figure 5C, $p > 0.7$, $p > 0.6$ and $p > 0.34$ for each measure).

During early washout after learning in VE1, the hand path areas are similar between subjects of the G1 and G2 groups (Figure 5B, $p > 0.1$), while the initial direction for the G1 group is higher than that of the G2 group ($p < 0.05$). However, the final directions are similar between the two groups ($p > 0.1$). This implies that the subjects of group G1 made significantly more corrections to their movements (through means such as online feedback or motor planning adjustments) compared to subjects of the G2 group. In the late washout trials, the G1 group’s hand path is adjusted such that it is similar to that of the G2 group for all three measures ($p > 0.05$, $p > 0.1$ and $p > 0.9$). The initial and final directions of the hand paths of both groups are not significantly different from zero ($p > 0.05$, $p > 0.46$ for the G1 group and $p > 0.25$ $p > 0.2$ for the G2 group), suggesting that the subjects return to the straight line.

The G2 group’s learning strategy results in the difference between the hand and the cursor path area $S^E$ is analyzed in Figure 6. The G2 group exhibits a nearly instantaneous change when either VE1 or VE2 is introduced. The change is maintained throughout the trials within the respective environment. On the other hand, the G1 group exhibits a gradual change in visual environment VE1 in the direction opposite to the change made by the G2 group in the same environment.

To further analyze this behavior, an exponential model is fitted to the data, where $y$ represents the difference between the hand and cursor path area $S^E$, $k$ is the generated trial number and $a$, $b$, and $c$ are the coefficients of the fit. The initial learning behavior of the subject is reflected in the sum of coefficients $a$ and $c$. The late learning behavior is reflected in the coefficient $c$. Finally, the learning rate of the subject is reflected in the coefficient $b$. The three coefficients of interest $a + c$, $b$, and $c$ are significantly different between the two groups.

The coefficient $a + c$ is low for the G1 group in VE1 and is not significantly different from zero ($p > 0.8$). For the G2 group in VE1 and VE2, the coefficient is significantly positive (with $p < 0.01$ and $p < 0.05$, respectively). This reflects the instantaneous increase observed for the G2 group’s learning behavior, which is not observed in the G1 group.

The learning rate $b$ of the G1 group is significantly negative ($p < 0.05$), while the G2 group’s learning rate in VE2 and VE1 after the increase is not significantly different from zero ($p > 0.6$ and $p > 0.1$, respectively).

The coefficient $c$, which reflects the steady-state of the subjects’ learning behavior, is significantly negative for the G1 group ($p < 0.05$) and is significantly positive for the G2 group in VE2 ($p < 0.05$).

Finally, the coefficients $a + c$ and $c$ for the G2 group in VE1 are significantly different from that of the G1 group ($p < 0.01$ and $p < 0.01$, respectively), but are similar to their values in VE2 ($p > 0.2$ and $p > 0.05$, respectively).

These results reflect the observation that subjects in the G2 group learn to move both in VE2 and VE1 by switching to another movement, and subsequently maintain the movement in the environment. By contrast, subjects in the G1 group gradually change their movements in VE1, resulting in a gradual convergence to the final movement trajectory in VE1.

**Discussion**

This study examined whether prior training with task-relevant feedback affects the learning strategy used in task-irrelevant environment. Two groups of subjects (G1 and G2) learned target reaching movements in the task-irrelevant environment VE1, where the G2 group had trained previously in the task-relevant environment VE2. The results exhibited two distinctly different behaviors for the two groups, suggesting that the learning strategy was affected by previous training. In particular, the learning strategy in the task-irrelevant environment VE1 was affected by previous training in the task-relevant environment VE2. In addition, the large variations in the number of trials necessary to complete a learning phase observed in the different subjects suggested that the observed behavior was independent of the total number of trials made by the subjects. The following sections further discuss the observed behavior.

**Humans use different learning strategies for the same task.**

When presented with the lateral visual deformation of VE1, the G1 group moved in the direction opposite the deformation and tended to drift further away from the target over trials. In contrast, the G2 group tended to move either in a straight line or in the same direction as the cursor in VE1, with the hand movements following the cursor movements (Figure 5 A.4-A.6).

The different learning behaviors can be explained by the different strategies employed by the two groups to learn the task. The G1 group may use visual reflexes to gradually compensate for the observed mismatch between the cursor and the straight line joining the starting point and the target trial after trial, as was proposed in previous works (Franklin et al., 2008; Krakauer et al., 2000), resulting in hand moving opposite to the direction of the cursor deformation.

On the other hand, the G2 group’s learning strategy seems to consist of switching their planned movements (Ganesh and Burdet, 2013) (Figure 6), resulting in their hand either ignoring or following the cursor (Figure 5 A.4-A.9). This strategy results in the hand either moving along a straight line or moving in the same direction as the cursor, enabling limited deviation of the hand from the two trajectories.

**Comparison of learning strategies.** The different learning strategies are further evidenced by the different learning behaviors made by the two groups in VE1. The G1 group’s learning strategy results in the difference between the hand and the cursor path area to decay exponentially after an initial jump. This is shown from the negative coefficient “$b$” of the G1 group in environment VE1 (Figure 6). Consequently, the hand gradually drifts from the straight line trajectory. Drifting was also observed when visual feedback was prevented during the movement (Brown et al., 2003; Salain et al., 2009). However in that case no exponential decay was observed, implying that the behavior was not associated with learning.

The G2 group’s learning strategy results in the difference between the hand and the cursor path area to change almost instantaneously when the subject is presented with the novel visual environment VE1 (Figure 6, right column). The fact
that the coefficient $b$ found for G2 group's movements in VE1 is not significantly different from zero in Figure 6 suggests that no significant adjustment of the hand or the cursor is made in the subsequent trials.

### Learning strategies affected by task-relevant errors

Although the G2 group's learning behavior was different from that of the G1 group in VE1, it was similar to the G2 group's learning behavior in VE2 (Figure 6). This suggests that the G2 group used the same learning strategy in VE1 as that used in VE2, which was a different strategy than that of the G1 group in VE1. It is therefore possible that the human subjects changed their strategy while learning to move in VE2.

A possible reason for the change is that if subjects use the strategy of the G1 group to correct for the visual discrepancies in VE2, then task-relevant errors are produced (Franklin et al., 2008), resulting in the endpoint cursor deviating from the target. The subjects are therefore forced to use visual reflexes and voluntary visual corrections to adjust the movement online in order to ensure that the hand reaches the target, which is evident in the final direction observed in the G2 group in the field (Figure 5A.6).

This reliance on visual reflexes caused the subjects to switch their planned movement, which allowed them to choose either to ignore or to follow the visual disturbances in VE2 in order to maintain a relatively straight trajectory and succeed in the task, as was observed in Figure 5 A.4-A.6.

In this light, reaching the target has a higher priority (the primary task) than compensating for the visual deformations (the secondary task), which is ignored if it conflicts with the primary task.

Over trials, it seemed that the subjects became familiarized with the new plan such that they relied less on online adjustments. This is supported by observations that the movements of the G2 group are invariant in probe trials, in which no cursor is provided to the subjects (Figure 5C), which implies that the movements in late learning are feed-forward in nature.

Overall, these observations suggest that task-relevant errors not only affect subjects' movement and visual reflexes, but also change the learning strategy employed, resulting in subjects using different feed-forward commands to achieve the task in the same visual field (Figures 5 and 6, VE1 environment).

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 experience (Kagerer et al., 1997; Sajio and Gomi, 2012).

Current results show that experience can further 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.

### Preference of gradual learning strategy

In VE1, it was observed that both learning strategies enabled the subjects to succeed in target reaching. Why did the subjects prefer the gradual adaptation strategy over the plan switching strategy, which they used only if they had been trained in the task-relevant environment VE2? Gradual change of the movement can be performed automatically after trial, for example by incorporating visual reflexes experienced in previous trial. This control strategy does not require much online control. In contrast, the strategy used in the task-relevant environment requires switching to another motor plan and coordinating the motor command with the ongoing movement and thus heavily relies on sensory feedback and online computation and control. Therefore, humans may use an Occam's razor approach for learning (MacKay, 2003) in that they do not attempt to make abrupt switches between plans for learning an environment, unless it is necessary to perform the task, since such a strategy is more difficult than gradually updating the feed-forward command using visual errors.

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**References**


Figure 1
Figure 2

- Null Field Task Irrelevant Environment (VE1) Probe Trials
- Task Relevant Environment (VE2)
- Null Field

Group 1
- Starting Phase Max Score: 30
  - Max Score: 25
  - One probe trial every 10 trials
- Learned Phase
- Washout Phase Max Score: 20
- Null Field

Group 2
- Starting Phase Max Score: 30
  - Max Score: 25
  - One probe trial every 10 trials
- Learned Phase
- Washout Phase Max Score: 20
- Null Field

Learning Phase
- Max Score: 25
- Learned Phase
- Max Score: 25
- One probe trial every 10 trials
- Washout Phase
- Max Score: 20
- Null Field

Figure 3

- (A) (B) (C)
- Cursor
- Hand
- $\alpha^H$, $\beta^c$
- $\alpha^C$
- $\beta^H$
- $\alpha^c$
- $\beta^c$

Null Field

(A) (B) (C)
Figure 4
Figure 5
Figure 6

Difference between hand and cursor path area

\[ \Delta = D - C \]

Fitting

\[ y = \alpha e^{\beta x} + c \]

* p<0.05
** p<0.01
*** p<10^{-3}

Fitted Coefficients

\[ a \]

\[ b \]

\[ c \]

* p<0.05
** p<0.01
*** p<10^{-3}
Figure Legends

Figure 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 hand position.

Figure 2. Experiment protocol.

Figure 3. Definition of the hand and cursor path area \( (S^H \text{ and } S^C) \), the initial hand and cursor direction \( (\alpha^H, \alpha^C) \) and the final hand and cursor direction \( (\beta^H, \beta^C) \), as defined in Equations (3) through (8).

Figure 4. Evolution of cursor trajectories (solid yellow to red lines) and hand path (solid blue to purple lines) for two representative subjects in groups G1 and G2. The different effects of VE1 and VE2 are observed in the first two columns, while the influence of learning of VE2 on the learning in VE1 is observed by comparing the first and third columns. Because the cursor is aligned with the hand in the null, probe and washout trials, only the hand paths are plotted. Since the robot stops recording when the hand paths velocity falls below 0.03 m/s, there are minute discrepancies between the cursor and the target at the end of the movement in VE1.

Figure 5. Comparison of behaviors across population

Figure 5a. Mean and standard deviation of the three measures for the hand (blue solid line) and the cursor (red solid line) across the normalized trials for all subjects. The different phases are shown in the alternating green and blue shades. The trials made by each subject are spline-fitted and 200 trials are generated in each phase, thereby enabling comparison of the performances of different subjects.

Figure 5b. Comparison of learning performances during the first and last 10 movements made by the two groups in visual environment VE1. The asterisks `*` indicate the significance level over all subjects. The graph compares the average measure made by the subjects of different groups across early and late learning trials and washout trials. The bars in the graph show the mean of the average measures of each group while the error bars provide the standard deviation.

Figure 5c. Comparison of learning performances during late learning and probe trials for the two groups in visual environment VE1. The asterisks `*` indicate the significance level over all subjects. The mean and error bars are calculated in the same way as described in Figure 5b.

Figure 6. \( S^E = S^H - S^C \) measure for the G1 and G2 groups in VE1 and VE2. An exponential fit of the measure against the normalized trial number is used to determine the coefficients \( a, b, \) and \( c \) shown on the right. For the fit, \( y \) is taken as the measure \( S^E \) while \( k \) is the generated trial number.