Adaptation to visual feedback delay in a redundant motor task

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Abstract

The goal of this study was to examine the reorganization of hand movements during adaptation to delayed visual feedback in a novel and redundant environment. In most natural behaviors the brain must learn to invert a many-to-one map from high-dimensional joint movements and muscle forces to a low-dimensional goal. This spatial "inverse map" is learned by associating motor commands to their low-dimensional consequences. How is this map affected by the presence of temporal delays? A delay presents the brain with a new set of kinematic data and, because of redundancy, the brain may use these data to form a new inverse map. We consider two possible responses to a novel visuomotor delay. In one case, the brain updates the previously learned spatial map, building a new association between motor commands and visual feedback of their effects. In the alternative case, the brain preserves the original map and learns to compensate the delay by a temporal shift of the motor commands. To test these alternative possibilities, we developed a virtual reality game in which subjects controlled the two-dimensional coordinates of a cursor by continuous hand gestures. Two groups of subjects tracked a target along predictable paths by wearing an instrumented data glove that recorded finger motions. The nineteen-dimensional glove signals controlled a cursor on a two-dimensional computer display. The experiment was performed on two consecutive days. On the first day, subjects practiced tracking movements without delay. On the second day, the test group performed the same task with a delay of 300 ms between the glove signals and the cursor display, while the control group continued practicing the non-delayed trials. We found evidence that to compensate for the delay, the test group relied on the coordination patterns established during the baseline, e.g. their hand-to-cursor inverse map was robust to the delay-perturbation, which was counteracted by an anticipation of the motor command.
INTRODUCTION

Sensory – motor adaptation is an essential aspect of motor control since the properties of our bodies and our environment change both over long and short time scales. To maintain a desired performance, the neural controller must be robust to these ongoing alterations. During the past two decades, several studies have demonstrated the ability of the sensory-motor system to adapt to different types of perturbations. These included force fields (Shadmehr and Mussa-Ivaldi 1994), visuomotor transformations brought by wearing optical prisms (Redding and Wallace 1988), and rotation and scaling of visual feedback (Krakauer et al. 2000; Mazzoni and Krakauer 2006).

Most of the earlier studies have focused on altering spatial and force information, while temporal distortions have been less extensively probed (Miall and Jackson 2006; Miall et al. 1985; Miall et al. 1993). The slow transmission rate of sensory information within the nervous system causes significant delays in the sensory motor loop. The delays are also variable depending on sensory pathways (e.g. proprioceptive, visual, acoustic etc.) To preserve correct haptic perception and motor control, the brain must compensate for the effects of variable delays. It is therefore plausible that the brain would be able to adapt also to an externally imposed delay in the sensory motor loop.

The task in the current study was characterized by a high degree of kinematic redundancy, with 19 signals mapped into 2 cursor coordinates. The most important goal in a remapping task is to learn how to embed the controlled space within the articulation space. The ability of the motor learning system to perform such remapping operation was investigated by Mosier and colleagues (2005) who asked subjects to control the position of a cursor by changing the configuration of
their fingers to reach targets that appeared randomly on the screen. Although the task did not explicitly specify any particular trajectory, subjects expressed a trend toward straighter paths of the controlled cursor. This trend suggested that subjects learned a motor representation of the Euclidean space over which finger movements were remapped. Using a same experimental approach, Liu and colleagues (2011) reported that the central nervous system compensates in two different ways for distorted cursors position by either a rotation or scaling transformation; subjects developed a new coordination pattern in compensating for the rotation, but relied on the patterns established during baseline practice to compensate for the scaling. In the current study, we instructed subjects to track a target, which moved in different directions on the screen. This task specified not only the position to be reached by the cursor, but also the time at which each position was to be attained. The task allowed us to investigate how the introduction of a visual feedback delay affects the inverse hand-to-cursor mapping. When facing the delayed target, subjects were exposed to a new set of sensory-motor data, concerning the positions of the visual cursor and the configurations of the hand gestures. Since the hand to cursor map is redundant, there are many, virtually infinite, “inverse maps” that a subject can use to decide which hand gesture to use for attaining a desired cursor positions. It is then plausible that, when facing a new set of sensorimotor data, subjects derive through practice a new inverse map. Alternatively, if the map is sufficiently stable, they may keep the original inverse map and compensate for the temporal delay by what amounts to an equivalent anticipatory response. Here, we present some new findings that favor the second hypothesis, supporting the robustness of the inverse map in face of a temporal delay injected along the visuo-motor chain.

MATERIALS AND METHODS
Fourteen neurologically intact right hand dominant subjects (mean age 26±6, 5 females) participated in the experiment and were randomly assigned to a test (n=7) or an aged matched control (n=7) group. All subjects were naive to the purposes of the study and provided written informed consent approved by Northwestern University’s Institutional Review Board. Each subject wore a right-handed cyber glove (Immersion, San Jose, CA). The cyber glove captures the movement of each finger joint: flexion of the phalangeal joints (proximal, middle, and distal), abduction of the thumb and fingers, and wrist flexion/extension and abduction/adduction, via 19 resistive sensors. Data from the glove were sampled at the rate of 50Hz.

The 19- dimensional vector of the sensor values was mapped on to the 2-dimensional (x,y) coordinates of a computer screen using a linear transformation (Mosier et al. 2005)

\[
\mathbf{p} = \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} a_{1,1} & a_{1,2} & \ldots & a_{1,19} \\ a_{2,1} & a_{2,2} & \ldots & a_{2,19} \end{bmatrix} \begin{bmatrix} h_1 \\ h_2 \\ \vdots \\ h_{19} \end{bmatrix} + \begin{bmatrix} x_0 \\ y_0 \end{bmatrix} = \mathbf{A} \mathbf{h} + \mathbf{p}_0
\]

Where \( \mathbf{p} = [x \ y]^T \) is the cursor location on the screen (endpoint space), \( \mathbf{h} = [h_1 \ \ldots \ h_{19}]^T \) is the glove signal vector (articulation space) and \( \mathbf{A} = [a_{i,j}] \) is a matrix of mapping coefficients (hand to cursor map). \( \mathbf{p}_0 = [x_0 \ y_0]^T \) is a constant matrix that aligns the mean value of calibration points to the coordinates corresponding to the center of the screen. We adopt the notation to indicate vectors in lower-case and matrices in upper case characters.

Before starting the experiment, in order to determine the coefficients of the hand to cursor map \( (\mathbf{A}_{2\times19}) \) we asked subjects to move all their fingers in a free-form spontaneous pattern – an activity which we called ‘finger dance’ – for about one minute. We used principal component analysis (PCA) to derive a set of orthonormal axes capturing the distribution of finger movement.
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Variance. Eigenvectors of the first and second PCs formed the hand-to-cursor transformation for each individual subject: the first two PCs mapped the high dimensional articulation space into the vertical and horizontal axes of the screen respectively. Furthermore the loadings were scaled to insure that every point within the workspace could be comfortably reached. In this framework, each hand posture corresponded to a unique point on the screen, while each screen location was mapped into a continuous subspace of “equivalent” hand postures.

Experimental Protocols

Subjects seated 0.5 m in front of a screen, wearing a cyber-glove. Each participant attended two one-hour sessions held across two consecutive days. At the beginning of each trial, subjects were asked to hold the cursor with the diameter of 0.4 cm inside a circle with the diameter of 1.4 cm. Hereinafter, this circle is referred to as the “moving target”. After the cursor was inside the moving target for about 2s, the moving target started to move toward one of three “stationary targets” that appeared in a random order on the screen (Fig. 1). Subjects were instructed to maintain the cursor inside the moving target until it reached one of the stationary targets. Each trial started from the same initial position and subjects could rest anytime between trials. The first session consisted of 10 epochs, in each epoch subjects performed 30 center-out trials, 10 for every movement direction. Subjects gained a positive score (on scale of 0 to 30 in one-point increments) if they succeeded in maintaining the cursor inside the moving target for more than 80% of the trial time.

The second session consisted of 11 epochs. Control subjects followed the same protocol of the previous day. The test group had the same configuration of the first session in the first two epochs in order to reinforce the learned baseline mapping of the previous day. The epochs 3 to 9
had delayed visual feedback. In these trials the position of the cursor on the screen was delayed by $\tau = 300\text{ms}$.

$$p = Ah(t - \tau) + p_0$$

In the last two "wash-out" epochs the delay was removed.

**Data Analysis**

The signals from 19 sensors of the cyber glove, the coordinates of the cursor, and the center of the moving target were acquired during the experiment and used for further analysis.

1) **Tracking error:** Tracking error for a single trial was defined as the cumulative Euclidean distance between the center of the cursor and the center of the moving target from the start of the trial until the moving target reached the stationary target. Tracking errors were then averaged across all 30 trials in a single epoch. The value obtained for all epochs from each subject were then normalized by the first epoch and averaged across all subjects in each group.

2) **Instantaneous error:** Tracking error (as defined in the previous paragraph) was employed to investigate the performance over the entire duration of a trial. Instantaneous error, however, was defined as the Euclidean distance between the center of the cursor and the center of the moving target at each time sample. This metric was used to detect performance changes within a trial. The values obtained for each time sample were averaged across all trials in a single epoch and across all subjects in the test group. Therefore, for each epoch, the instantaneous error was a function of time that represented the temporal evolution of the error within a trial (in contrast, the tracking error for a trial was a single number).
3) Smoothness of the movements: Jerk or the second derivative of the speed profile is used in the literature as a standard measure to quantify human movement smoothness (Flash and Hogan 1985). We calculated the jerk as in (Smith et al. 2000):

\[ J = | \sum_{k=1}^{n} \dddot{x}(t_k) | \]  

Here, \( t_k \) corresponds to discrete samples of a single trial. A fifth order Savitzky-Golay polynomial filter was used to smooth and attain the second derivative of the speed profile for each trial. The value obtained for all epochs from each subject were averaged across all subjects in each group.

4) Movement variability: The articulation space had 19 degrees of freedom and the cursor moved in a two dimensional space. Thus, there exist and infinite number of possible hand movements to capture targets. A unique feature of this task is the ability to clearly distinguish between the degrees of freedom that contribute to kinematic performance and those that do not. This is analogous – in simplified linear terms - to the concept of controlled and uncontrolled manifolds (Scholz and Schöner 1999). The Moore-Penrose pseudo-inverse of \( A \) allows us to decompose the map into a “task space operator”, \( h_T \) and a “null-space operator”, \( h_N \):

\[ h_T = A^+ A h \]

\[ h_N = (I_{19} - A^+ A) h \]  

Where \( A^+ = A^T (AA^T)^{-1} \) and \( I_{19} \) is the 19-D identity matrix.

To calculate variability in the task and null space, glove signals corresponding to all trajectories toward each target in a single epoch were projected back into the task and the null space. The
variance of the projected data were calculated at each time sample and then averaged across all
samples and across all subjects in each group.

5) Inverse map: The metric we used to quantify the extent to which visual feedback delay
induced change of the inverse hand-to-cursor map is similar to the metric used by Liu and
colleagues (2011). Let \( P = [p_1, p_2, \ldots, p_T]^T \) denote a matrix containing the sequence of \( T \) cursor
locations in a certain epoch, and \( H = [h_1, h_2, \ldots, h_T]^T \) the corresponding glove signals; then the
estimated inverse hand-to-cursor map \( B_{est} \) is derived by the following equation:

\[
B_{est} = HP^T(P^TP)^{-1}
\]

We calculated the \( B_{est} \) for three epochs of the second session: the first two baseline epochs
(\( B_{BL1} \) and \( B_{BL2} \)) and the last delayed epoch (\( B_{adapt} \)). The cursor location was transformed
during the delayed epoch. Therefore, to investigate whether the inverse map is completely
changed or it is just modified by the delay, we compute \( B_{adapt} \) by considering the actual
coordinates of the cursor, not its delayed representation. We evaluated the difference in
magnitude between the two baseline epochs and the difference in magnitude between the inverse
map obtained at the end of adaptation (\( B_{adapt} \)) and the baseline inverse map using the following
equations:

\[
\Delta B_{noise} = ||B_{BL1} - B_{BL2}||
\]

\[
\Delta B_{adapt} = ||B_{adapt} - B_{BL2}||
\]

If \( \Delta B_{adapt} \) were significantly larger than \( \Delta B_{noise} \) one should reject the hypothesis that the
inverse map is stable in the face of a delay.
6) Distance between the null space components of the hand postures:

A complementary approach is to investigate the null space components of the hand postures corresponding to a same location in the endpoint space before and after adaptation. If subjects applied an inverse transformation to the baseline map, then the null space components of the hand posture corresponding to a no delayed position of the cursor (not the delayed cursor seen by the subjects) would be equal to the null space components of the hand posture at the same position in a baseline trial. On the contrary, if subjects created a new inverse map during adaptation then the null space components of the two hand postures would be different.

Ten equally spaced via-points between and excluding the initial position and center of each stationary target were selected. We extracted the corresponding hand postures when the cursor was at the minimum distance from these points. We didn’t include observations in which the minimum distance exceeded 1.4 cm to minimize the task space variability. Three last epochs of the first day together with the first epoch of the second day were considered as a reference. From these reference data we calculated - using Equation (3) - the null-space components of each hand posture and derived their mean, $\mu$, and the covariance, $C$. We considered four epochs as a reference to have enough observations to derive the covariance matrix from data. We used these reference values to estimate how the hand configurations varied during the remaining epochs. To this end, we used the Mahalanobis distance (Jerde et al. 2003; Pesyna et al. 2011) which is a variant of the Euclidean distance, weighted by the covariance of each vector component. In our case, indicating by $x$ the null-space component of a hand posture, its Mahalanobis distance between $x$ and the reference value $\mu$ is
This is effectively an adaptation of the z-score to N-dimensional vector spaces. Here, we calculated the average Mahalanobis distance between the null-space hand posture components in the reference epochs and in the following epochs.

### Statistical Analysis:

Statistical analysis on task performance and variability were performed using a 2 × 2 (epoch × group) mixed-model ANOVA with epoch as a within-subject factor and group (test, control) as a between subject factor. An independent sample t-test was used to compare the performance and task/null space variability of the two groups at the end of the experiment. Additionally, we used an independent sample t-test to examine between-group differences of the Mahalanobis distance.

A paired sampled t-test was employed to analyze changes in the task/null space variability of the control group in day two of the experiment and task/null space variability of the test group in delayed epochs. We also used a paired sampled t-test in the analysis of the inverse map to compare baseline with late adaptation. The threshold of significance in all the analysis was set at 0.05.

### RESULTS

#### Task performance

In the first day, subjects learned to control a cursor on the computer screen by coordinated finger movements. With training, all subjects improved their performance in the tracking task (Fig.2A). A 2×2 (epoch × group) ANOVA between epoch 1 of the first day and epoch 2 of the second day revealed a significant decrease in tracking error (main effect of epoch, $F_{1,12} = 122.96, \ p < 0.001$) and a significant increase in movement smoothness with practice (Fig.2B, main effect of
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There were no difference in performance and learning rates between the two groups; no group effect (tracking error: $F(1,12) = 1.02, p = 0.331$, smoothness: $F(1,12) = 1.30, p = 0.276$) and no interaction effects.

When the delay was introduced, the tracking error for the test group increased and the smoothness decreased. With practice, test-subjects adapted to the perturbation. A 2x2 (epoch x group) ANOVA between early (epoch 3 of the second day) and late (epoch 9 of the second day) delayed epochs for the test group and corresponding epochs for the control group found main effects of epoch (tracking error: $F(1,12) = 5.52, p = 0.037$, smoothness: $F(1,12) = 24.86, p < 0.001$) and main effect of group (tracking error: $F(1,12) = 14.31, p = 0.003$, smoothness: $F(1,12) = 23.62, p < 0.001$) and no interaction effects for the tracking error. An interaction effect was present for the smoothness; $F(1,12) = 17.34, p = 0.001$). Learning of the kinematic mapping between hand configuration and cursor position progressed during the second day of the experiment for the control group. At the end of the experiment, when the delay was removed (epoch 10 of the second day), the performance of the two groups was not significantly different (tracking error t-test: $p = 0.58$, smoothness t-test: $p = 0.73$).

To investigate the task performance within each trial, we calculated the instantaneous error (Fig. 2C). The zero of the time axis corresponds to the time at which the target starts moving. At the beginning of each trial the cursor and the moving target were at the same position and thereby the error was small. During the very first epoch of the experiment since the subjects have not learned how to control the cursor, the error kept growing as the moving target was approaching one of the stationary targets. However, after a few blocks of training, the general shape of the error curve became more consistent across epochs. At the beginning of each trial, the error increased with a constant slope because of the reaction time needed to respond to the target's
movement. After the subjects started moving in the direction of the target, the tracking error decreased until a steady state value. With the introduction of delay, the cursor started moving 300ms after the subjects initiated to track the target. Because of this, the peak in the error shifted by 300ms with respect to the previous epoch and the error increased uniformly over the entire trial. With adaptation there was a uniform decrease in the error.

Figure 3A, represents the average speed profiles across all subjects in the two groups. Control subjects (red) and test subjects (blue), attempting to track the target moving at a constant speed (black). At the beginning of the second session, before the introduction of the delay, the two groups had the same performance level as shown by speed profiles and the trajectories of two representative subjects (Fig. 3 left panel). Immediately after introducing the delay, test subjects displayed large oscillations in the speed profile (Fig. 3A second panel) and the trajectories became more variable as well (Fig. 3B, second panel). At the end of the training period, test subjects have reduced the oscillations in the speed profile (Fig. 3A, third panel) and the variations in the trajectory (Fig. 3B, third panel). However, the performance was still less accurate compared to the control subjects (Fig 3A and C, third panel). Upon the removal of the delay, subjects in the test group did not exhibit a significant change in the speed profile (Fig. 3A, right panel) and the variance of the trajectories continued to decrease (Fig 3B, right panel).

Null space – task space variability

A 2x2 ANOVA between the first and last epoch of the first day indicated that all subjects significantly reduced both the task (main effect of epoch, F (1,12) = 62.86, p < 0.001 and no group effect, F (1,12) = 0.81, p = 0.39) and the null space (main effect of epoch, F (1,12) = 79.48, p < 0.001 and no group effect, F (1,12) = 0.98, p = 0.34) variability in the first session.
Throughout the second day, the control subjects were practicing the same task of the first day and they kept decreasing their task and null space variability. Paired t-test between the first and the last epochs of the second day for the control group found significant reduction in both the task and null space variability (task space: $p = 0.006$, null space: $p = 0.029$).

There was no significant group effect in the first two epochs of the second day, before the delay. When the delay was introduced, test subjects failed to track the moving target appropriately and the variance in the task space increased, reaching a peak in epoch 4 (Fig. 4). Therefore, the difference has reached a peak in the second delayed epoch rather than immediately after the introduction of the delay. Paired t-test between two sets of trials before (epoch 2 of the second day) and after (epoch 4 of the second day) introduction of the visual feedback delay shows that test subjects exhibited a main effect of the training phase for the task space variability ($p = 0.042$).

The null space variability also increased with the introduction of the delay, but the difference between training and baseline performance was close to threshold of significance only during epoch 4 ($p = 0.052$). Increased variance in the task space simply shows subjects’ errors in performing the task and indicates that during early adaptation, subjects failed to track the moving target appropriately. Furthermore, the cursor position at any particular time varied from trial to trial. Increased variance in the null space with the introduction of the delay can have different interpretations. One interpretation is that the null space contribution to command updating increased upon introduction of the delay suggesting that subjects were exploring the null space to build a new inverse model of the hand-to-cursor mapping so as to compensate for the perturbation. Another possibility is based on the observation that, due to the physiological couplings between the articulations of the hand, it is not feasible to activate the degrees of
freedom that are contributing to the task independently from the remaining degrees of freedom.

In other words, the controlled space is embedded in the articulation space in such a way that it is impossible to increase the variance in task space without producing a similar effect in null-space.

Immediately after the delay was removed (epoch 10 of the second day), the two groups had same task and null space variability and there was no significant difference between the two groups (task space t-test: $p = 0.38$, null space t-test: $p = 0.52$).

**Distance between inverse maps**

When subjects perform the tracking task, they effectively solve an ill-posed inverse problem, by finding the high dimensional hand configuration corresponding to the low-dimensional target location. Since the cursor position is connected to the hand configuration by the matrix $A$ of Equation 1, the simplest way to represent the subject's learning task is to find a matrix $B$ that fulfills the requirement of placing the cursor in the target. This implies that $B$ must be a right-inverse of $A$, that is $A \cdot B = I_2 = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}$. We estimated this right inverse as described in the methods section by least squares regression on glove and cursor data, as described in the Methods section (Equation 4).

Figure 5A illustrates the extent to which $B_{\text{est}}$ changed during the adaptation to the visual feedback delay. For the test subjects $\Delta B_{\text{adapt}}$ did not exceed $\Delta B_{\text{noise}}$ (paired t-test: $p = 0.46$). This finding is consistent with the hypothesis that test subjects did not change the internal representation of the map - i.e. they kept the same right-inverse of $A$ - and canceled the temporal perturbation with an anticipatory response.

**Distance between hand postures**
The estimate of the $B$ matrix is based on the assumption that the subjects construct an internal model based on a generalized right inverse of the linear map. To avoid limiting our analysis to such linear model, we considered how the subjects modified the control of the degrees of freedom that did not have a direct impact on task performance. To this end, we calculated the Mahalanobis distances between the null space components of the hand postures in epochs 2 to 11 of the second day with respect to data of the four preceding baseline epochs (Fig 5B).

There is not a significant difference between the two groups in the epoch before the delay (t-test: $p = 0.2$). With the introduction of the delay, the Mahalanobis distance from the baseline null-space tends to increase for the test group. This distance also increased slightly for the control group due to the fact that learning progressed during the second day: the control group improved in task performance (Fig. 2) and had less movement in the null space (Fig. 4) by the end of the second session.

In the late adaptation epoch (epoch 9 of the second day) there was no significant effect of learning the delay between the test group and the control group on the Mahalanobis distance to the baseline null-space (t-test: $p = 0.33$). In early-perturbation trials although, the peak shows a deviation from the baseline inverse map, subjects tend to preserve the inverse map that they had acquired in the early baseline practice.

*Time course of adaptation and after effects – trial by trial analysis*

When the delay was first introduced, test subjects could not know that the perturbation was applied and therefore, there was a significant increase in the tracking error. With training, subjects gradually learned to compensate the delay by anticipating the motion of the target that is by compensating the temporal delay via an inverse transformation. To investigate the time course
of transition from the non-specific compensation to the anticipatory compensation, we looked at the performance of test subjects during the first 200ms after the onset of the movement. The onset of the cursor movement was established as the time at which the cursor exited the starting zone, so as to avoid including in the analysis the reaction time from the onset of the target movement. Figure 6A, shows the tracking error in this interval, with each data point indicating the average error across three consecutive trials. Paired t-test between the first and last three delayed trials indicates a significant reduction in the initial tracking error with training ($p = 0.001$).

When the delay was removed, subjects in the test group did not exhibit evident after-effects. There was a sharp decrease in the tracking error when the delay was removed (epoch 20) rather than an increase in the error, which is typically observed after adaptation in other studies. To minimize the epoch averaging effect, we have compared the tracking error between the last three adaptation trials and the first three washout trials for all subjects in the test group (Fig. 6B). There was not a significant difference between the two sets of tracking errors (paired t-test: $p = 0.30$). Taken together, these results support the conclusion that the inverse map acquired during the baseline training was robust to the temporal perturbation caused by the injected visuo-motor delay.

**DISCUSSION**

The objective of our study was to investigate how subjects compensate for the temporal visuomotor transformation caused by the introduction of a delay between the movement commands and their observable consequences. We addressed this question in a motor remapping paradigm, where subjects controlled a cursor and performed a tracking task by moving their
fingers. The map from the articulation space (the configuration of the finger captured by 19 data
glove signals) to the task space (the 2 coordinates of the cursor and of the moving target on the
computer monitor) had 2 key features; it was a redundant map since a multitude of finger
configurations – virtually infinite – correspond to a single position of the cursor. In order to
move the cursor to a target, subjects needed to solve an inverse ill-posed problem (Bertero et al.
1988) and they could learn the map in infinite possible ways, because of the abundance of the
right inverses of the mapping matrix. Due to its nature, the map was entirely novel for the
subjects.

The remapping paradigm offers a unique opportunity to investigate how the central nervous
system learns to operate within a novel geometrical environment. Here, we considered
specifically how the learning of a spatial map is affected by adapting to a temporal delay. We
have tested a range of delays when designing the experiment and found that 300 ms was
approximately the longest delay that subjects could overcome. We considered two possibilities:

a) Subjects would learn to associate the instantaneous image of the cursor with their motor
command. This would induce a new representation of the map between cursor positions and
finger configurations.

b) Alternatively, subjects would maintain the static map between cursor and finger position and
would simply learn to cancel the temporal lag of the display by applying a corresponding lead to
the finger configuration.

Our findings support the second hypothesis and refute the first. According to the first hypothesis,
after training with delayed feedback, when we restored the baseline condition by suddenly
removing the delay, we would expect to observe some after-effect with an increase on tracking
error. In contrast, we failed to see such an after effect even in trial-by-trial analysis. Furthermore, the analysis of the tracking error revealed that there were not significant differences within and between groups when looking at the performances before and after the practice in the delay condition. These observations are in contrast with the formation of a new map during the exposure to a delay, as this map would have likely interfered with the map previously acquired without a delay. These results confirm that subjects compensate the visual feedback delay by a time shift of their motor commands, without altering the representation of the hand-cursor map acquired by practicing without delay.

The delay drastically increased the tracking error and decreased the smoothness of the movements. But subjects showed a clear adaptation. Subjects in this study relied on the inverse map established during the baseline practice to compensate for the delay as subjects exposed to the scaling distortion in another experiment (Liu et al. 2011). However, the adaptation to visual feedback delay was significantly slower than the adaptation to scaling perturbations. The adaptation to scaling, indeed, was almost completed within a set of 108 trials, whereas our findings show that after 210 trials subjects were not able to completely regain the level of performance in the non-delayed trials. This slower adaptation to temporal delays is in agreement with the findings of Foulkes and Miall (2000). In the scaling perturbation, the coordinates of each point in space is multiplied by a constant. Therefore, there is a uniform expansion or shrinkage of the space. Although the delay perturbation in the current study was constant in time, its spatial effect was velocity dependent and non-uniform. In other words, in the presence of fixed time delay, the shift in the position is determined by the velocity which increases the uncertainty in the subject’s estimate of the cursor position. It has been shown that rates of adaptation also depend on uncertainty of the feedback (Izawa and Shadmehr 2008; Wei and
Furthermore, slower adaptation could also be produced by the unconventional action-consequence correspondence caused by the delay.

Learning of the kinematic mapping between hand configuration and object position progressed promptly during the first day and resulted in decreased tracking error and increased smoothness of the movements. Subjects reduced complexity in the overall coordination of finger motions by presenting a strong and progressive decrease of variability in task space and null space. This is in agreement with the result obtained in similar studies (Casadio et al. 2010; Liu et al. 2011; Mosier et al. 2005). While our findings may be inconsistent with the idea that the motor system shifts its variance to the null space (Latash et al. 2001; Todorov and Jordan 2002) one should consider that those earlier studies did not involve performing a task within a novel geometrical environment. An inexperienced subject first must learn a stable inverse map from desired behavior to motor commands. This requires, identifying the task-relevant and task-irrelevant components of a movement and also removing variability in the latters. Once this inverse map is formed, then the variability can be redirected toward the null space by effectively shifting the motor commands within a system of equivalent inverse maps (Kawato 1999; Wolpert and Kawato 1998). Moreover, in a complex task, such as the one in this study, when the task is still challenging, subjects might tend to seek a single solution rather than exploit the null space to minimize the effort, thus the null space variability do not decrease.

It is important to consider two issues in our interpretation of the results. One issue is whether the variables that we employed to assess the robustness of the baseline map against the delay (i.e. the difference between the norms of the inverse maps and the distance between the null space components of the hand postures) were sensitive enough to capture small changes that may have occurred with the introduction (or removal) of delay. Although there were small changes in both
variables, we used a statistical approach and looked for changes that were above and beyond the
natural variability observed during the no-delay task. A second issue is whether the
dimensionality of the task had an influence on the results. We selected a 19-to-2 map to provide
a high level of redundancy with many possible alternative solutions (which presumably gave
participants flexibility to change their inverse map). Nevertheless, we found that the participants
preserved the original map. However, it might be possible that high dimensionality actually
increased the cost of finding a new solution leading to participants preserving their initial
solution. Further experiments are required to find whether the current conclusion still holds for
simpler low dimensional maps.

In summary, our results confirm that subjects adapted to visual feedback delay but that the space
representation built during the baseline trials was robust to the delay perturbations and the
process of adaptation to delay did not affect the learned spatial map.

GRANTS

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DISCLOSURES

No conflicts of interests, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.M.I. and A.F. conception and design of research; A.F. performed experiments; A.F. analyzed
data; A.F., R.R., M.C., and S.M.I. interpreted results of experiments; A.F. prepared figures; A.F.
REFERENCES


FIGURE CAPTIONS

Fig. 1- Schematic representation of the task. After holding the cursor at rest at the starting position for 2s, the moving target started to advance toward one of the stationary targets. Subjects were instructed to keep the cursor inside the moving target until it reached the stationary target.

Fig. 2- Task performance. A, Normalized tracking Error. B, Absolute cumulative jerk. Dashed line indicates separate days and gray area includes epochs with delay. Error bars represent standard error. C, Average instantaneous error within a trial.

Fig. 3- Average speed profiles across all subjects and trajectories of two representative subjects. A, speed profiles of control subjects (red) and test subjects (blue) tracking the target moving at a constant speed (black). B, Trajectories of a test subject. C, Trajectories of a control subject.
Fig. 4- Task-space and null-space variability as a function of epoch number. Dotted lines and solid lines represent the null-space and the task-space variance respectively. Dashed line indicates separate days and grey area includes epochs with delay. Error bars represent standard error (between-participant). GSU: Glove Signal Unit.

Fig. 5- Analysis of kinematic performance in the second session. A, Variation of $B_{\text{adapt}}$ from baseline to last delay epoch ($\Delta B_{\text{adapt}}$) compared with the variation across baseline epochs ($\Delta B_{\text{noise}}$). B, Mahalanobis distance between the null space components of the hand postures of the epochs 2 to 11 of the second day with respect to data of the four previous epochs. Grey area includes epochs with delay and error bars represent standard errors. GSU: Glove Signal Unit.

Fig. 6- Trial by trial analysis. A, Average tracking error during the first 200 ms after the movement onset of all subjects in the test group. Each data point represents the average error across three consequent trials. Shaded region illustrates the standard error. B, Average tracking error during the last three adaptation trials and the first three washout trials of all subjects in the test group. Each dashed line represents an individual subject.
Figure 1
Figure 2
Figure 5
Figure 6

A.

B.