

Feedback and feedforward adaptation to visuomotor delay during reaching and slicing movements

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Abstract

It has been suggested that the brain and in particular the cerebellum and motor cortex adapt to represent the environment during reaching movements under various visuomotor perturbations. It is well known that significant delay is present in neural conductance and processing; however, the possible representation of delay and adaptation to delayed visual feedback has been largely overlooked. Here we investigated the control of reaching movements in human subjects during an imposed visuomotor delay in a virtual reality environment. In the first experiment, when visual feedback was unexpectedly delayed, the hand movement overshoot the end-point target, indicating a vision-based feedback control. Over the ensuing trials, movements gradually adapted and became accurate. When the delay was removed unexpectedly, movements systematically undershot the target, demonstrating that adaptation occurred within the vision-based feedback control mechanism. In a second experiment designed to broaden our understanding of the underlying mechanisms, we revealed similar after-effects for rhythmic reversal (out-and-back) movements. We present a computational model accounting for these results based on two adapted forward models, each tuned for a specific modality delay (proprioception or vision), and a third feedforward controller. The computational model, along with the experimental results, refutes delay representation in a pure forward vision-based predictor and suggests that adaptation occurred in the forward vision-based predictor, and concurrently in the state-based feedforward controller. Understanding how the brain compensates for conductance and processing delays is essential for understanding certain impairments concerning these neural delays as well as for the development of brain-machine interfaces.

Introduction

It is generally accepted that internal models facilitate the control of fast arm movements in the presence of delayed sensory feedback (Wolpert & Miall, 1996; Wolpert *et al.*, 1998). Jordan & Rumelhart (1992) posit that the forward model, which acts as an estimate of the plant, can be used to train the inverse-model-based feedforward controller. This concept of linked adaptive inverse and forward models was proposed to explain adaptation of reaching movements in the presence of novel force fields (Bhushan & Shadmehr, 1999) but not during adaptation to visuomotor delay.

In this study, we tested whether the brain compensates and adapts to changes in a feedback loop delay in a similar manner using a pair of linked models. This is significant because it is still a matter of debate how delay is learned in the motor system (Pressman *et al.*, 2012). It is known that feedback delays may be affected by luminance intensity (Purushothaman *et al.*, 1998; Kammer *et al.*, 1999), kinematic properties of the visualised object (Whitney & Murakami,

1998), age (Thomas & Lambert, 1960; Dorfman & Bosley, 1979; Stetson *et al.*, 1992), and obesity (Nathan *et al.*, 1992). Therefore, understanding how motor control adapts to delay may also contribute to our understanding of sensorimotor integration (Kording *et al.*, 2004; Miyazaki *et al.*, 2005) and visual illusions such as the flash-lag effect (Krekelberg & Lappe, 2001; Nijhawan & Kirschfeld, 2003).

To test our hypothesis about delay compensation, we devised a method based on adaptation to visuomotor delay during reaching movements. We compared the effects of this delay on rhythmic and discrete movements and examined the generalisations between them. Previously, Krakauer *et al.* (2000) used rhythmic movements to compare adaptations to visual gain change and visuomotor rotation, and Mazzoni & Krakauer (2006) used them to compare learning strategies during visuomotor rotation. These movements were also used to support a motor control model with two separate feedforward controllers to explain generalisations between reach and rapid reversal movements during visuomotor rotation (Scheidt & Ghez, 2007), but they have never been used during adaptation to visuomotor delay.

We hypothesised that introducing delay bias into the feedback loop would result in a feedback adaptation tuned to the new delayed state. We further investigated the relationship between the feedback and feedforward controllers and whether they would adapt in parallel. We hypothesised that these two controllers are model-based; the feedback controller includes a forward model (an estimate of the plant), whereas the feedforward controller is an inverse model. Under these

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conditions, introducing a delay bias in the state feedback should lead to adaptation of the forward model, together with adaptation of the feedforward inverse-based model. Furthermore, when the forward controller learns a new delayed state, we predicted that at least some component of the feedforward controller should learn an earlier state.

Using our paradigm with a simulation of a computational model utilising stabilisation and trajectory controllers in series (Scheidt & Ghez, 2007) and feedback control (Wagner & Smith, 2008), we shed some new light on the adaptive mechanisms of the motor control system.

Materials and methods

Subjects

Twenty-one subjects who answered an advertisement enrolled in the study after signing a written informed consent form, as stipulated by the Institutional Helsinki Committee, Beer Sheva, Israel, conforming to The Code of Ethics of the World Medical Association. The subjects were all naive as to the study goals and were paid to participate. All of them had normal or corrected-to-normal vision.

Methodology

In this study, we carried out two experiments. The first was designed to examine the effects of visuomotor delay during reaching movements, and the second to evaluate the adaptation effects on trajectory and end-point during training in reach movements and transfer to rhythmic slice movements (Sainburg *et al.*, 1993) and vice versa. In these tasks, the visual feedback of a cursor during the movement was manipulated such that a fixed 70 ms delay was introduced between the actual end-point position and its visual representation.

Discrete and rhythmic movements differ in their kinematics. Rhythmic movements do not require stabilisation and have peak acceleration at the reversal point (Guiard, 1993, 1997; Buchanan *et al.*, 2006; Hogan & Sternad, 2007) as compared with discrete reaching movements that have zero acceleration at the end-point. The shortest primitive of rhythmic movement is a single out-and-back rapid movement, designated here as a 'slice.'

Our method was based on the introduction of a fixed visuomotor delay in the visual feedback loop during the reaching task, and subsequent inspection of the adaptation and generalisation between slicing (rhythmic) and reaching (non-rhythmic) movements. Using this method and a computational model, we showed that an error in a feedback-estimated state led to errors and gradual adaptation that can be explained by the notion of the feedback controller utilising an adaptive forward model and a feedforward controller. Furthermore, we present evidence that also supports the adaptation of the feedforward controller, possibly as a result of modification in the forward model. Although we do not address here the causality of events, it is consistent with the notion of a pair of controllers adapting together, as shown in Fig. 1.

Unlike other methods, such as visuomotor rotation (Krakauer *et al.*, 1999) and force field perturbation (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994), visuomotor delay changes only the feedback state of the system, and preserves all other aspects of the movements such as the required trajectory or end-point. Subjects can potentially perform the task successfully by sending a nominal motor command and ignoring the visual feedback. We argue that this is a critical issue, as trajectory alterations, or end-point modifications, require corresponding *a-priori* modifications of the feedforward controller that are the result of different required joint angles and recruitment of different motor units. Furthermore, as torques are related to joint angles, we would expect there to be changes in the hand dynamics and in the

required co-contraction throughout the movement. Under these conditions, adaptation may be attained only if at least some of these feedforward properties are tuned differently from their initial null conditions.

Experimental setup and apparatus

With the right hand, subjects held the handle of a SensAble Phantom[®] Desktop[™] haptic device (Geomagic, Wilmington, MA, USA) in a virtual augmented reality system (Fig. 2A) while performing two-dimensional reaching or slicing movements towards a 1 cm cross-shaped visual target located straight ahead, 12 cm from a constant start position presented on a high-frequency 118 Hz CRT screen (model VCDTS23957-2E, ViewSonic, Walnut, CA, USA) with a screen resolution of 1024 × 768. The position of the haptic device was sampled at 1000 Hz using an independent haptic loop. During special conditions when visual cursor feedback was delayed by 70 ms, its location was estimated based on exact time measurements and a linear position interpolation of the two measured events that occurred just before and just after the required delay. Hand movements were limited to planar movements by a virtual surface that the subjects were instructed to move upon. Wrist movements were constrained by a wrist splint. During the reach, the subject received visual feedback in the form of a virtual sphere of 1 cm in diameter that was aligned with the end-point location of the Phantom device stylus. Direct visual feedback of the arm was obscured by an opaque screen and a drape that covered the upper shoulder.

Experiment 1: adaptation to visuomotor delay

In this experiment, each of eight subjects was required to perform a reaching movement while observing a virtual sphere aligned with his/her hand. Each of these movements began with the subject holding the cursor steady over the start position for a period of 1 s. A visual cursor color change cue instructed the subject to initiate the movement. The subject was instructed to move rapidly and smoothly (in a single movement), and as accurately as possible towards the target goal. The start and end-points alternated between trials; thus, subjects alternated between reaching outward (out) and reaching inward (back) (see Fig. 2BI and II, respectively). The trial was considered complete when the subject reached constant accuracy of 2 mm over the target center for a period of 0.5 s. The experimental protocol (Fig. 2CI) consisted of five sessions with 100 movements in each session. Each session lasted less than 10 min, with breaks of 5–10 min between sessions. The entire experiment lasted up to 90 min. The first block (100 trials) was used as a training session to enable the subjects to become acquainted with the Phantom device and experimental task. The data from the training session were not included in the analysis. In the remainder of the sessions, the visual feedback was either non-delayed (designated N) or delayed by 70 ms (designated D) for the entire duration of the movement. The 70 ms delay was based on preliminary measurements showing the inability of subjects to distinguish between delay and non-delay conditions and was also based on a similar value reported by Smith & Bowen (1980). Furthermore, visuomotor delay of this magnitude was previously shown to be indistinguishable by subjects while actively moving a hand (Leube *et al.*, 2003), or while perturbed involuntarily (Shimada *et al.*, 2005). The N and D conditions were either constantly imposed (block trials) or pseudo-randomly interspersed in the block (rare catch trials): delayed catch trials during N block (designated Dc) and non-delayed catch trials during D block (designated Nc). The block order (N, D) was counter-balanced between subjects. After the training session, the experiment included three additional

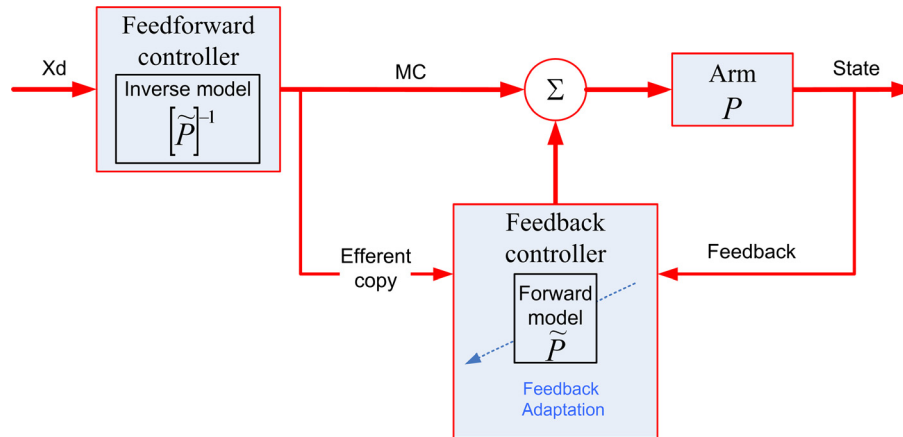


FIG. 1. Simplified schematic representation of the motor control system controlling an arm with feedforward and feedback controllers. The feedforward controller converts the desired trajectory into a motor command (MC), whereas the feedback controller integrates the MC with sensory feedback for predicting motor outcome and for compensating for errors in real time. The feedback controller may use a forward model \tilde{P} , which is an estimate of the arm (P); the model is adapted according to the discrepancy between the efference copy and the feedback. The feedforward controller can then use this inverse of the estimate \tilde{P}^{-1} for computing the appropriate MC given the desired trajectory.

sessions. A baseline session consisted of 150 baseline condition trials (N or D, depending on the group), followed by a session of 200 trials with alternate conditions (D or N, respectively), which ended with a short baseline session of 50 trials. The timeline of trials is depicted in Fig. 2CI. Upon completion of the experiment, each subject answered a brief questionnaire designed to determine whether the delayed vision condition was consciously perceived.

Experiment 2: delay visuomotor generalisation between reaching and reversal movements

Thirteen subjects initially participated in the experiment, but results are reported for 10; one participant was dropped due to a data-recording failure, another because he was unable to perform the rapid slice movements as required, and the third left the study of his own accord. Subjects were instructed to perform either reaching or slicing movements, depending on the target color cue, to a target positioned 12 cm from the starting position. The 10 subjects were randomly assigned to one of two groups. One group performed reach adaptation and transfer to slice movements (Fig. 2CII), and the other adaptation to slice and transfer to reach movement (Fig. 2CIII).

Prior to each trial, a robot moved the subject's hand to a fixed starting position. At some random time afterwards (up to 1.5 s), a target appeared and the subject was required to perform either a reaching movement (Fig. 2BII) or a rapid reversal (slicing) movement to the target (Fig. 2BIII). This idea was inspired by the work of Scheidt & Ghez (2007). Feedback of the hand location via a cursor on a screen was provided continuously as soon as the hand moved 1 mm from the starting position. In pseudo-random vision, omitted trial cursor feedback was not provided for the entire movement duration. We were concerned that the velocity of movements would increase with practice or fatigue and that uncontrolled velocities (as in the first experiment) would generate different overshoot effects that would be more difficult to simulate using a computational model. Therefore, we provided subjects with feedback on the initial movement velocity after the hand had moved 3 cm away from the starting position. Correct velocity was defined as 0.45 ± 0.05 m/s. The subject received feedback on his/her speed performance at the end of the trial after stabilising at the target for 2 s, with different colors coding the velocity performance in the form of a long rectangular shape located at the top of the screen (Fig. 2BIV; green with a

smiley, correct; filled red, too fast; filled blue, too slow). During the reaching movement, each subject was instructed to move the center of a cross-shaped cursor into a target and hold his/her hand stationary at the end-point until the trial ended, at which time the robot moved the hand without cursor feedback to the starting position. The subjects were instructed to remain passive during the active movement of the robot. For slice movements, subjects were instructed to move the cursor to the center of the target, reverse the direction without pausing at the target, and then stop exactly at the initial position, marked with a cross. Following completion of the slice, velocity performance feedback was provided on the basis of the same velocity criteria as for the reach. We were concerned that, instead of a continuous slice, the subjects might actually perform reach-away and reach-back movements, thus impeding our attempt to inspect generalisation from cyclic (slice) to discrete (reach) or vice versa as the movements would be similar. Guiard (1993, 1997) addressed the difference in control of repetitive aiming movements and claimed that cyclic limb motion is not constructed from a string of discrete segments. Later, Buchanan *et al.* (2006) presented an analytical method that uses the difference in the kinematic properties to show whether a movement is cyclic or not. Others (Levy-Tzedek *et al.*, 2010) also used this method. We assumed that fast reversal movements would tend to be cyclical, and validated this post-trial. We provided additional post-trial feedback aimed at preventing the occurrence of reach movements during slice (to the extent possible) as well as providing feedback about the accuracy of the reversal point. The feedback, in a form of a sphere with the same dimensions as the cursor, appeared at the reversal point, which was defined as the maximum radial displacement from the home target in the outward phase of the movement. The feedback icon was white if the movement was quick and sharp or red if it was not. We established the timing requirement that the last 20% of the movement trajectory before and after the reversal point should last no more than 0.15 s, or else the slice movement was considered to be too slow, and appropriate feedback was given. Cursor and task performance feedback (i.e. velocity or slice accuracy) were not provided during omitted trials, so as to prevent trial-by-trial adaptation as a result of this feedback. Subjects performed 10 blocks of trials lasting about 10 min each, with 5 min breaks between them. In total, this experiment lasted up to 3.5 h. Each block consisted of 100 trials; the first five blocks consisted of reaching and slicing movements without visuomotor delay, whereas

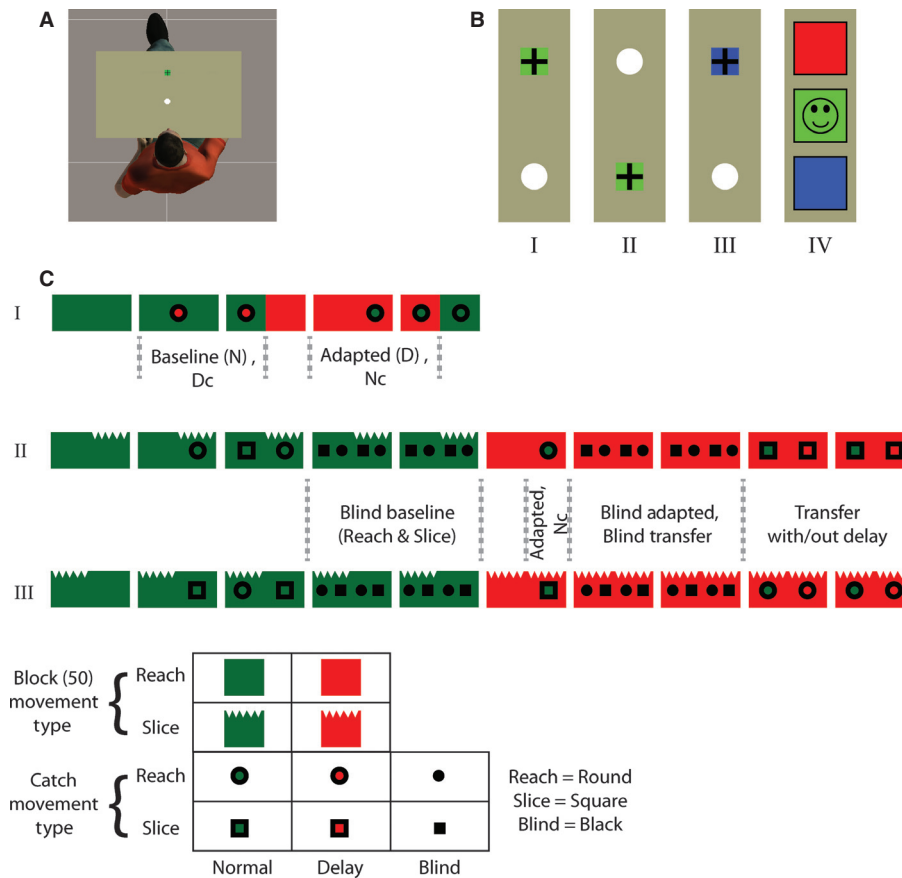


FIG. 2. Schematic description of experimental setup. (A) A seated subject performed planar movements while grasping the stylus of the robotic phantom arm. The hand was obscured at all times by an opaque screen and apron. (B) During active hand movement, a white circular cursor followed the phantom location on a high-frequency monitor screen (118 Hz); the cursor location was either delayed or not relative to the true hand location, depending on the trial condition. Distance from the starting location to the target was always 12 cm and target and cursor sizes were 1 cm. In the first experiment, reach movements alternated between out-and-back movements (BI and II), whereas in the second experiment, movements were either reach or slice depending on target color (BI and III, respectively), and always aimed away with a passive return by the robot. In the reach condition, the subject was instructed to reach from an unseen starting location and stabilise the hand at the green target, whereas in the slice movements, the subject was instructed to perform a rapid slice movement toward the blue target without pausing at the reversal. In all movements, subjects received post-trial feedback on the velocity of the movement (BIV), encouraging them to keep the required velocity of 0.45 ± 0.05 sm/s (see text for further details). (C) Symbolic representation of experimental protocols showing the number of blocks, breaks, and movement/vision conditions within each block (see Table 1 for details). The first experiment protocol (CI) included five blocks of 100 trials of reach movements with short breaks between blocks. Two sub-groups performed this experiment. The first sub-group initially learned to reach without visuomotor delay and then the effect of delay on the trajectory was tested prior to adaptation during catch trials (Dc) and after repetitive exposure (D). Finally, catch trials without delay (Nc) were randomly presented during delay block in order to observe after-effects. The other sub-group performed a counter-balanced block order of the delay conditions. The second experiment protocol (CII & CIII) consisted of 10 blocks and two groups of subjects. Each group was trained during reaching (CII) or slicing (CIII) movements with visuomotor delay, whereas transfer to the other movement was tested with or without vision. The trial condition sequence between groups was identical apart from the movement condition, which was the mirrored version of the other.

the remaining blocks were administered with a constant visuomotor delay of 70 ms. The sixth block was a training block with a single movement type. The remaining blocks were mostly blocks of trained movements with pseudorandom catch trials (on average almost every sixth trial) of two types (vision-omitted trials and zero-delay catch trials of the untrained movement). The omitted trials were presented in the two blocks following the adaptation block, and the last two blocks contained the zero-delay catch trials. The omitted trials were used to assess the performance of the system without visual state feedback error, whereas the zero-delay catch trials were used to verify that the subjects had adapted to the delay. During omitted trials, subjects were instructed to move exactly as they had in the normal trials. During experiments with adaptation to the opposite movement type, the sequence of movements was mirrored (i.e. instead of a reach movement, a slice movement, and vice versa), but the delay order remained unchanged (Fig. 2CII and III).

Data analysis

The hand position was measured by the built-in Phantom encoder via Reachin[®] software (Hasselby, Sweden) and a dedicated C++ code. The encoder sampling rates in the first and second experiments were 1000 Hz, whereas the actual position was saved at every refreshing rate of the screen (118 Hz). Further analysis was performed with Matlab R2010a. Velocity profiles were extracted by differentiation of the collected position points, and onset of movement was defined as the time point at which each velocity profile exceeded 5% of peak velocity. Mean trajectories were aligned relative to movement onset (defined as 5% of the peak velocity) and then, for each time point, a mean value and SEM were computed. We further performed a repeated-measures ANOVA analysis during specific time points with the subjects as a random factor to inspect the phenomena of visuomotor delay on reaching accuracy at the end-point (Experiment 1) or reversal

TABLE 1. The four different hypotheses

Hypotheses	Predicted "No Vision" Trajectories	Simplified Models
Proprioception Remapping I		
Feedforward Adaptation II		
Feedback Adaptation III		
Feedforward & Feedback Adaptation IV		

Each row presents a possible working hypothesis. The center column presents the predicted omitted trial trajectories for each working hypotheses (see text for further details). Curve color-coding is as in Fig. 2 and gray dashed horizontal line marks distance to target. The right column presents a simplified schematic of the equivalent model with red dashed line marking the specific block where adaptation occurs. We predict different trajectories for reach and slice adaptation only in the feedforward and feedback adaptation (bottom row).

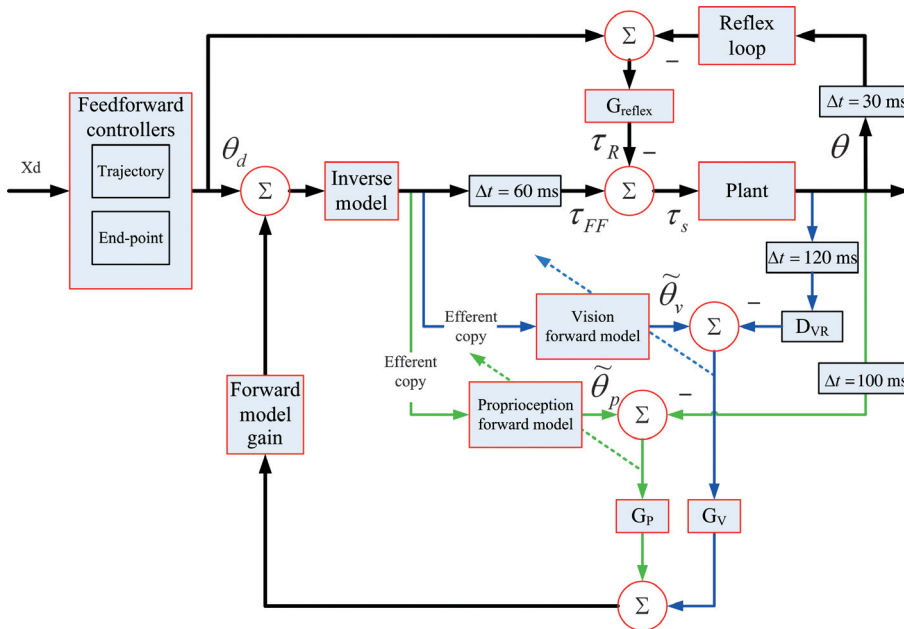


FIG. 3. Dual shared internal models for feedback and feedforward adaptation. The feedforward system includes two controllers in parallel, one responsible for the trajectory and the other for stabilisation. Each modality (green, proprioception; blue, vision) has its own forward model that receives an efference copy as an input and predicts the hand state. The prediction is compared with the feedback, which is then used in real time to correct the movement planned trajectory and also to enable trial-by-trial adaptation of the forward model. The block contains the artificial imposed delay. The other delays are identical to those of Wagner & Smith (2008) with the addition of a 100 ms delay for the proprioception loop delay (Cordo *et al.*, 1994).

point (Experiment 2). When we found a significant effect, we performed a post-hoc Tukey *t*-test to compare performance across conditions and factor levels. Effects were considered statistically different at the $P = 0.05$ level. The differences are reported as the mean and SE. Specific details are provided separately in each part of the Results.

Possible adaptation strategies

On the basis of a pilot study, we hypothesised that, during initial exposure to delayed visuomotor feedback, subjects would react on-

line to the delayed vision, thus over-reaching the target before returning the hand to the correct end-point position. Furthermore, we hypothesised that, with sufficient practice, subjects would adapt to this delayed vision feedback.

Theoretically, such a phenomenon of adaptation to delay could be explained by a number of different adaptive mechanisms. Therefore, we first inspected the possible theoretical explanations and then dismissed them one by one by inspecting movement kinematics in our experimental protocol of adaptation to reach and transfer to reversal movement

(slice) and vice versa, with or without visual feedback. When required, we used computational modeling to support our findings. We considered four adaptive mechanisms that will lead to differences in motor performance during the vision-omitted catch trials as exemplified in Table 1: (I) end-point proprioception remapping (Bernier *et al.*, 2005), (II) single feedforward controller adaptation, (III) single feedback controller adaptation, and (IV) adaptive feedforward and on-line feedback controllers tuned inversely (Bhushan & Shadmehr, 1999) (see also Fig. 3).

The proprioception remapping hypothesis assumes that the proprioception will shift further away from the true hand position such that the vision-delayed position, when integrated together with proprioception according to a previously described maximum likelihood estimator (Ghahramani & Wolpert, 1997; Van Beers *et al.*, 1999; Ernst & Banks, 2002), will be accurate; hence, during the vision-omitted condition, both adapted movement types should overshoot the end-point target (Table II). The second option assumes that a single feedforward controller will gradually adapt to the feedback's on-line overshoot error by shortening its pre-planned command; thus, during the vision-omitted condition, we expect to observe undershoot of the target during both movement types, with or without a gradual sub-movement return to the target position in the reach condition (Table III). The third option, the feedback adaptation hypothesis, assumes that the feedback controller will adapt its reaction to the visual delayed feedback until the overshoot phenomena ceases; hence, during the omitted vision feedback condition (when there is no visual input to the feedback controller), we expect to observe trajectories similar to those of the pre-adaptation condition during reach and slice movements (Table III). Finally, a mutual feedback and feedforward adaptation based on internal models should result in changes in both controllers. We further considered the possibility that the feedforward controller has two distinct components: trajectory and end-point stabilisation controllers, with dominance of the latter in approaching the final movement (Scheidt & Ghez, 2007). As we expect that, during all vision-delayed feedback conditions, the final hand position will be aligned with the target (whether or not there was a corrective sub-movement before the alignment), we would not expect the desired end-point feedforward component to adapt. Instead, we suggest that the overshoot movement during exposure to visuomotor delay would be adapted by an earlier initiation of the stabilisation controller, which would diminish the overshoot error. Our predictions about the vision-omitted trial trajectories for this hypothesis are based on our model and simulations. The extent predictions of the trajectories are different for the reach adaptation and slice adaptation groups and are summarised in (Table IV).

Model and simulation

Our model is based on the mutual feedback and feedforward hypothesis, and it explains the experimental findings by using a pair of feedback controllers and a pair of feedforward controllers (Fig. 3). We suggest that this model is probably fundamental for various movements, including both reaching and slicing movements. The vision and proprioception modalities use two independent forward controllers for estimating the state of the limb in modality-specific coordinates. This topology provides redundancy, as well as other advantages (see further details in the Discussion). The two sensory estimations, $\tilde{\theta}_p$ and $\tilde{\theta}_v$ (for proprioception and vision, respectively), are compared with the incoming afferent states and the resultant prediction errors (Wolpert *et al.*, 1995) are utilised to issue a corrective action to the feedforward controller, which drives the plant on-line (Wagner & Smith, 2008), and to adapt the corresponding sensory forward model. We assume that the feedforward controller is an inverse

version of the forward model (Jordan & Rumelhart, 1992; Bhushan & Shadmehr, 1999); hence, a change in the forward controller should also manifest in the feedforward controller. However, as our hypothesis includes two separate feedforward controllers [end-point and trajectory (Scheidt & Ghez, 2007), each with specific synchronicity requirements], visuomotor delay may lead to different effects on these controllers. Specifically, Scheidt & Ghez (2007) showed that reach movement during visuomotor rotation adaptation yielded overshoot trajectories during transferred slice movements. These can be explained if the feedforward controller initiates the stabilisation controller during the slice reversal process although this is not actually required during slice movement, thus leading to extra production of torques that results in the observed overshoot. Using a simulation, we will show that the timing of these two controllers alters post-reach adaptation either as a result of adaptation in the forward model or as an attempt to decrease overshoot at the end of the movement during exposure to visuomotor delay.

During the pre-adaptation condition, we expected that the forward model-based feedback controllers and the feedforward controllers would be tuned to the task parameters and that the forward model prediction for each modality would accurately predict the appropriate state; therefore, there would be no prediction errors. However, during the initial exposure to the delay perturbation, the unaltered state prediction of the vision-forward model precedes the delayed feedback state. Thus, the vision prediction error overdrives the plant, causing an overshoot trajectory under the delay catch (Dc) condition. The hand then returns and stabilises at the original desired end-point. The prediction error adapts the forward model accordingly, such that, after sufficient repetitive exposure, the delayed feedback is correctly predicted by the specific forward model, and as a result, the prediction error drops to zero and the trajectory becomes smooth, as before. The parallel proprioception control loop does not vary, as the proprioception prediction error in our model is not influenced by the visuomotor delay. Following adaptation, whenever the delay is abruptly removed (Nc condition), the vision-forward controller output state lags behind the actual feedback state, thus generating a negative prediction error that will drive the plant on-line to an undershoot position. The unchanged end-point controller will eventually drive the limb to the correct end-point.

Furthermore, our model predicts that the vision-omitted trial trajectories post-adaptation will be similar to the pre-adaptation trajectories of the same movement type as vision efference copy is not available to the vision-forward model in the vision-omitted trials, and there is no vision feedback signal for comparison. Consequently, the vision-forward model output will be null (Mehta & Schaal, 2002). Therefore, the movement is dominated by the unaltered proprioception loop, leading to smooth trajectories, similar to those in the vision trials. This conclusion is exemplified in (Table IV) where the baseline-trained omitted trajectories and post-adaptation omitted trajectories (of the same movement type) are identical.

During post-adapted conditions, the adapted forward vision controller predicts an earlier state relative to its baseline condition at a given time. Therefore, if the inverse model implements an inverse of this state-modified internal-forward model, it is expected that its properties might change as a result, with some component of this feedforward controller estimating an earlier state relative to the pre-adaptation condition. We can logically eliminate that these changes would occur in the end-point component of the feedforward controller; otherwise, the hand would not reach the goal position. Thus, during this condition, when the forward and inverse components are tuned again, we do not expect to observe overshoot errors in the adapted movement during the vision condition as the modified feedforward trajectory controller dominates the initial movement phase,

whereas the unmodified end-point controller dominates the stabilisation phase. However, overshoot errors will be evident if the end-point controller command is omitted. To validate this idea, we tested the transfer to slice movements that do not require stabilisation at the reversal point. Obviously, this test should be carried out during omitted trials, or else the expected end-point overshoot will cause a trial-by-trial adaptation that will eliminate this observation. The phenomenon is not expected to be symmetric between slice and reach training as, during delayed visuomotor slice training, visual feedback about the hand position clamps the trajectory error at the reversal point. Therefore, our model predicts that, after slice training, vision-omitted reaching movements will be as accurate as before, and there will be no evidence of hypermetria (Table IV, Slice Adaptation).

Finally, as reported earlier for force perturbation (Wagner & Smith, 2008), a forward model controller system can accurately predict a state roughly 350–400 ms after the onset of perturbation. We used this time estimation to show that the forward model delayed state can explain post-adaptation zero-delay catch trials. In brief, we performed a correlation analysis between individual trajectories of the same movement type before and following delay adaptation. Using the bootstrap method, we randomly compared pairs of trajectories and calculated the time lag that provides the highest correlation between the two. This provided a tool to estimate the time lag difference that best explains the difference between trajectories before and following adaptation. This analysis may also support the existence of adaptation in the forward model as the feedforward controller dominance diminishes and the feedback controller dominance increases during the course of the movement (Scheidt & Ghez, 2007; David *et al.*, 2009). Thus, removing the initial segment of the movement from the correlation analysis emphasises the contribution of the feedback controller.

We performed a set of forward dynamic numerical simulations to explore the model presented in Fig. 3. The simulation consists of three basic components: feedforward, feedback, and reflex control modules. The feedforward controller includes a separate control for trajectory and posture control, whereas the feedback loop includes two separate forward models, one per modality (vision and proprioception). The final control system is a hybrid of the control systems presented by Scheidt & Ghez (2007) and Wagner & Smith (2008) with the addition of two separate forward models, one for each modality. We incorporated the virtual visual delay by adding a delay

in the visual feedback loop during virtual delay trials. We assumed that adaptation to visual delay takes place in the visual forward module, which learns to predict the new delay state. We did not model trial-by-trial adaptation.

We modeled both movement types tested in the second experiment (reach and slice) using a minimum-jerk trajectory for the reaching movement and a special composition of two out-and-back reach movements for the slice (Scheidt & Ghez, 2007). These movements were carried out in a straight-line reaching movement of 12 cm in length, and duration was matched to the average group trajectory profile pre-adaptation. Movement originated from a position 0.4 m in front of the subject and was directed along the midclavicular line (3 cm to the left of the shoulder center of rotation).

The desired trajectories were transformed using inverse kinematics to joint angular movements required to achieve the desired trajectories. Inverse dynamics equations of motion of a two-link planar arm were used to calculate the required shoulder and elbow torques for facilitating these trajectories as defined by the calculated joint angles.

The anthropometric parameters used for simulating arm movements for a typical subject were based on previously published simulations by Scheidt & Ghez (2007) and Shadmehr & Mussa-Ivaldi (1994).

The inverse dynamics equation is comprised of two components. The first part (upper two lines) describes the resultant torques computed directly from the joint angles of the desired trajectory. The second describes the torques arising from a stabilisation controller around a desired reversal or end-point. These stabilisation torques are scaled by two multiplicative scaling functions, $\Phi_R(t)$ and $\Phi_E(t)$, that are given as sigmoid functions of time. Thus, these functions increase the contributions of the stabilisation torques to the movement torques towards the end of the movement, increasing the relative contribution of the desired end-point-related torques, and decreasing the relative contribution of the torques that are related to errors between the feedback and the predicted state. These switching functions are initiated (i.e. when the function equals 0.5) at the time of peak jerk in the outgoing phase during the reach and return phase during the slice. The functions can also be set to zero depending on the required action, e.g. during a reaching movement, $\Phi_E(t)$ is set to zero.

The resultant torques (T_{FF}) along with the feedback and reflex torques (T_R) were used to drive the plant using the forward dynamic equations of motion (i.e. the inverse of Eqn 1).

$$\begin{aligned}
 \begin{bmatrix} \tau_s \\ \tau_e \end{bmatrix} &= \begin{bmatrix} I_s + I_e + m_s r_s^2 + m_s r_e^2 + m_e l_s^2 + 2l_s m_e r_e \cos(\theta_e) & I_e + m_e r_e^2 + l_s m_e r_e \cos(\theta_e) \\ I_e + m_e r_e^2 + l_s m_e r_e \cos(\theta_e) & I_e + m_e r_e^2 \end{bmatrix} \begin{bmatrix} \ddot{\theta}_s \\ \ddot{\theta}_e \end{bmatrix} \\
 &+ \begin{bmatrix} 0 & -l_s m_e r_e \sin(\theta_e) & -2l_s m_e r_e \sin(\theta_e) \\ l_s m_e r_e \sin(\theta_e) & 0 & 0 \end{bmatrix} \begin{bmatrix} \dot{\theta}_s^2 \\ \dot{\theta}_e^2 \\ \dot{\theta}_s \dot{\theta}_e \end{bmatrix} + \begin{bmatrix} V_{11} & V_{12} \\ V_{21} & V_{22} \end{bmatrix} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} \\
 &+ \Phi_R(t) \begin{bmatrix} B^* \\ V_{21} & V_{22} \end{bmatrix} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} - [K^*] \begin{bmatrix} K_{11} & K_{12} \\ K_{21} & K_{22} \end{bmatrix} \begin{bmatrix} \theta_{s-\text{reach}} - \theta_s \\ \theta_{e-\text{reach}} - \theta_e \end{bmatrix} \\
 &+ \Phi_E(t) \begin{bmatrix} B^* \\ V_{21} & V_{22} \end{bmatrix} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} - [K^*] \begin{bmatrix} K_{11} & K_{12} \\ K_{21} & K_{22} \end{bmatrix} \begin{bmatrix} \theta_{s-\text{end}} - \theta_s \\ \theta_{e-\text{end}} - \theta_e \end{bmatrix}
 \end{aligned} \tag{1}$$

Inverse dynamic equation describing the torques associated with movement and stabilization. Each segment here was modeled as a homogeneous rigid body with mass m concentrated at the center of mass located at distance r from the proximal joint. Each segment i also had a moment of inertia I_i , where the index i is either s or e corresponding to shoulder and elbow respectively. The two upper lines describe the torques associated with movement while the other two lines describe the torques associated with stabilization. The $\Phi_R(t)$ and $\Phi_E(t)$ functions are essentially smoothed sigmoid functions that increase the contributions of the stabilization torques towards the end of the movement. For further details see Scheidt and Ghez, (2007).

The feedback loop also used a similar forward dynamics equation to simulate the forward module's predictions. We used two forward models, one for the proprioception and another for the vision model, to generate a predictive state that is unique for each modality. This architecture of two forward models has the advantage of redundancy and other important aspects that we address in the Discussion. The state output from these predictors was compared with the actual delayed output of the plant and the resultant errors were gained (see Gv and Gp in simulation schematics) and fed back to the input as a correction signal to drive the simulated limb in real-time using the second derivative of the state errors (Wagner & Smith, 2008). The individual gains were selected such that vision dominated during vision trials and was entirely eliminated during blind vision trials. Hence, gain during vision trials was set to 0.9 for the visual predictor and 0.1 for the proprioception predictor, whereas in blind trials only the proprioceptive estimates were used (i.e. vision predictor weight was set to zero).

Model validation included verification of the open loop controller, closed loop controller (visual/proprioception/both), and reflex loop torque contribution comparison in the forward/inverse dynamics module.

Results

Experiment 1: feedback adaptation

Feedback control rather than ballistic movement

We examined the trajectory profile in each direction separately as well as in both directions. During the non-delay condition, subjects generated smooth and accurate trajectories in both directions (Fig. 4A, green curves showing typical trajectories of one subject; Fig. 4B, average trajectories across subjects), but during the delayed catch condition, subjects over-reached the target before stopping at the end-point (Fig. 4A and B, red circles, curves). Using an ANOVA, we compared the extents of the non-delay block condition with the delay catch condition. The overshoot was statistically different during both the out and the back movements ($F_{1,7} = 103.68$, $P < 0.001$, 0.011 m; $F_{1,7} = 38.04$, $P < 0.001$, 0.01 m, respectively) and when collapsed together ($F_{1,7} = 136.47$, $P < 0.001$, 0.011 m). This observation suggests that visual feedback was used during the movement, i.e. that subjects did not exclusively employ a ballistic pre-planned movement, but rather used it together with an on-line feedback control.

Return to the null trajectory during constant visuomotor delay

Following continuous repetitive movements with visuomotor delay, subjects modified their trajectories, reduced the over-reaching pattern, and returned to a trajectory similar to that for the non-delay condition (Fig. 4A, B and D, red curves vs. green baseline curves). This finding suggests that the subjects were able to compensate for the visual delay either by learning gradually to ignore it, or by biasing their proprioception map at the end-point such that a joint estimate between vision and proprioception would lead to smooth movement, or by adapting to the use of the visual feedback through feedback adaptation.

Adaptation: significant after-effect in catch trials

In non-delayed catch trials during the delay block condition, subjects under-reached the target and immediately corrected their movement (Fig. 4A and B, green circle curves). This was significant

in the out, back, and collapsed directions ($F_{1,7} = 118.16$, $P < 0.001$, 0.008 m; $F_{1,7} = 36.33$, $P = 0.001$, 0.008 m; $F_{1,7} = 80.44$, $P < 0.001$, 0.008 m, respectively).

Figure 4C shows the average overshoot and undershoot with SE (at the same time of peak overshoot) per subject.

If subjects adapted their movements by learning to ignore vision, relying on proprioception alone, we would not expect to observe undershoot movements during the non-delayed catch trials. Instead, this result suggests that subjects adapted to the visual delay condition, i.e. that adaptation occurred in the visual feedback and its translation into a motor command. We further used these findings to reject the hypothesis that subjects used proprioception remapping during the adaptation to the delay by comparing the relationship between overshoot and undershoot amplitudes across subjects. If subjects had used proprioception remapping, then we would expect that subjects who experienced larger overshoot would experience larger undershoots. A linear regression analysis between the overshoot and undershoot amplitude across subjects did not reveal a significant slope; thus, we concluded that adaptation cannot be explained by proprioception remapping.

No conscious perception of visuomotor delay

A review of the questionnaires completed after the experiment by eight subjects revealed that six did not report spatial or temporal misalignment between the cursor and the hand at any given time. The other two subjects reported that, in general, they did notice a misalignment, but this was reported as being either constant across all trials or always smaller for the hand movement than for the cursor movement. In addition, both of these subjects reported that the target was occasionally displaced, which was never the case.

Experiment 2: transfer between movements indicates feedback adaptation

This experiment was designed to elucidate the details of the adaptation mechanism implied in the results of the first experiment. During this experiment, subjects were required to adapt to delayed visual feedback while performing either a reach or a slice movement. The transfer of the adaptation between movement types was investigated under these conditions, as well as in omitted feedback catch trials. This paradigm, which included the use of slice movements and the kinematic evaluation of the transfer between movement types, together with the computational model, provides a means to investigate where within the motor control the adaptation occurred as the cyclic slice movement, unlike the reach movement, does not require stabilisation at the reversal point. Although slice and reach movements have different kinematics, we can still compare the maximum vertical displacement at the reversal point and end-point, respectively, as a method of measuring the generalisation or transfer between movements.

Slice movements are kinematically different from reach movements

Subjects practiced two types of movement (reaching and slicing) under normal conditions and then adapted to visuomotor delay for one of the movement types. Following adaptation, generalisation to the other movement type was studied. Although subjects were instructed to perform slicing movements without pausing at the reversal point, we were concerned that they might act differently. Therefore, we analysed the slice movement performance using the method suggested by Guiard (1993, 1997) and Buchanan *et al.*

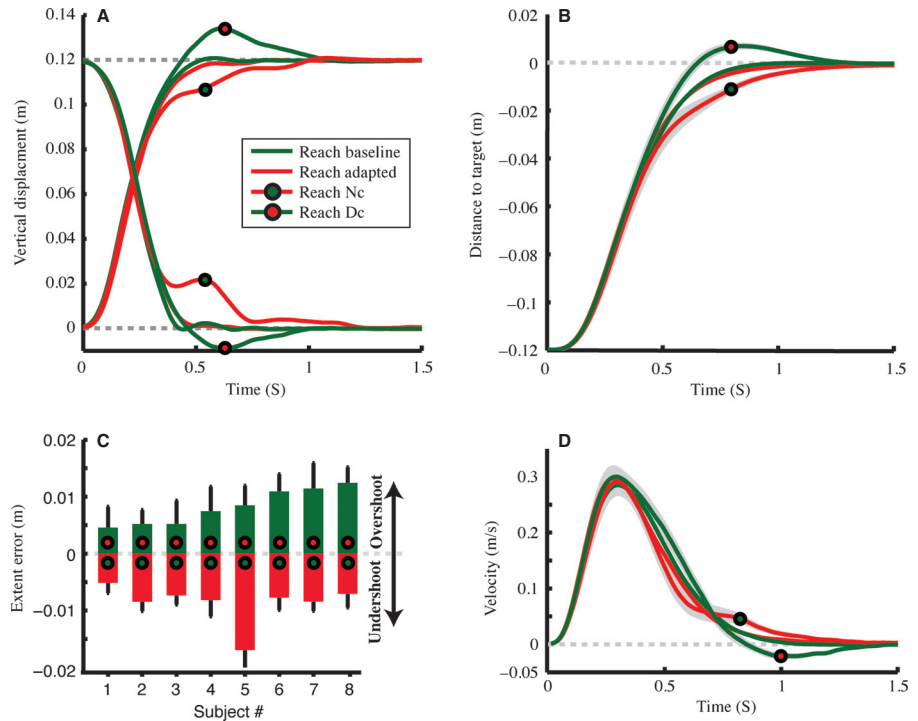
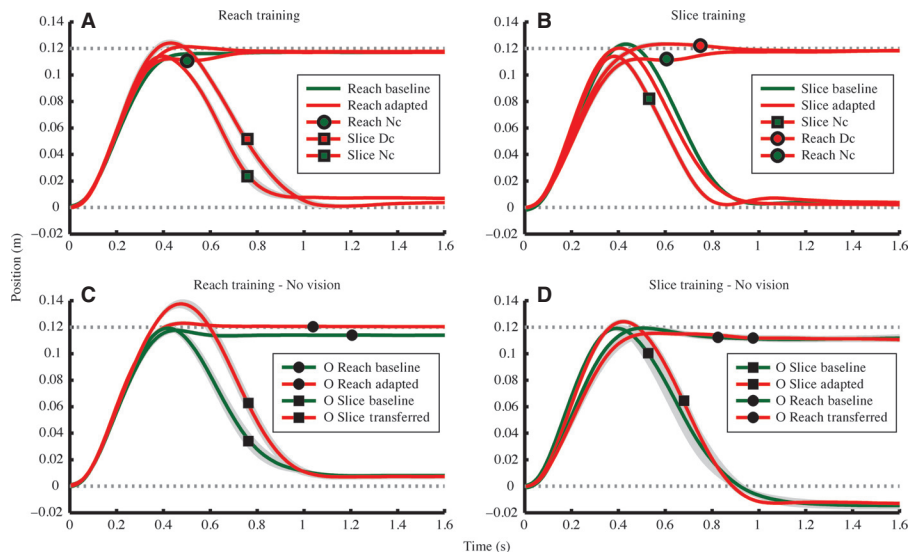


FIG. 4. Reaching with visuomotor delay. (A) Representative hand trajectories of a single subject in both reaching out and reaching back directions before and after adaptation to delay. The trajectories are smooth and accurate both before adaptation (reach baseline, green curves) and after constant exposure to delayed conditions (reach-adapted, red curves), but not under the same visuomotor delay conditions during catch trials (Reach Nc and Reach Dc). For the latter visuomotor delay conditions, the hand overshoot the target in the delayed catch trial in the non-delay block session, but undershot the target in the non-delayed catch trials in the delayed block session (Reach Nc). Gray dotted lines mark the position of the target and the starting position in the out-and-back movements. (B) Average overshoot and undershoot per subject. Values are averaged across out-and-back movements (colors as in A), ordered according to the overshoot amplitude. Black bars show SE. (C) Mean trajectories across subjects in delay and normal catch trials showing the overshoot and undershoot effects (colors as in A). Values are averaged across out-and-back movements. (D) Average velocities of the trajectories in B.

FIG. 5. Adaptation to delay and generalisation. Average trajectories with SE (gray) for two different subjects in reach adaptation and generalisation to slice (left column) and in slice adaptation and generalisation to reach (right column). Although slice and reach kinematics differ, we can compare the lateral deviation relative to baseline movements in order to evaluate adaptation and transfer. Adaptation is evident by comparing baseline condition to adapted condition (A and B, green curves vs. red curves without symbols), and also by observing the undershoot after-effect movement in the normal catch trial following adaptation (A, Reach Nc; B, Slice Nc). Undershoot after-effect is transferred symmetrically from reach to slice (A) or vice versa (B), as is evident from the similar undershoot amplitudes (A, Reach Nc vs. Slice Nc; B, Slice Nc vs. Reach Nc). However, omitted trials showed an overshoot effect during reach training and transfer to slice (C, red and green curve with square symbol), but not during slice training (D, red and green curve with filled circle). These results are similar to our predictions in Table 1–IV.



(2006). The results show that, in the overwhelming majority of the movements (slightly over 90%), subjects did not pause at all at the reversal point and, thus, performed a perfect slice. Occasionally, movements deviated from the perfect slice, and in this case, the movements were not included in the analysis. We defined a minimum index of harmonicity of 0.8 as a slice. More than 93% of the movements met this criterion, and the analysis is based on these movements. Our reported results, which show different adaptation during the omitted vision condition, also provide evidence that the slice movements are not composed of two discrete reaches.

Adaptation and transfer between movements

Figure 5 shows the mean trajectories and the SEs for a single subject reach adaptation and a different subject slice adaptation,

whereas Fig. 6 shows group mean trajectories and SEs for reach and slice adaptation.

To test whether adaptation took place, we measured whether zero-delay trials post-adaptation had a significant undershoot after-effect, as was evident in the first experiment. We performed a one-way ANOVA with each group (with subject as a random factor), comparing the mean movement extent before and after adaptation without delay (Figs 5A and B, Figs 6A and B, green vs. green square curves) at two specific times marked by a black arrow in Fig. 6. In both groups, the adapted movements showed a statistically significant effect ($F_{1,4} = 33.06$, $P < 0.005$, 7.5 ± 1 mm and $F_{1,4} = 9.9$, $P < 0.05$, 7.7 ± 2 mm for reach and slice movements, respectively). Thus, we concluded that adaptation did indeed take place.

To test whether transfer took place, we performed a similar analysis on transferred movements (i.e. zero delay before and after adap-

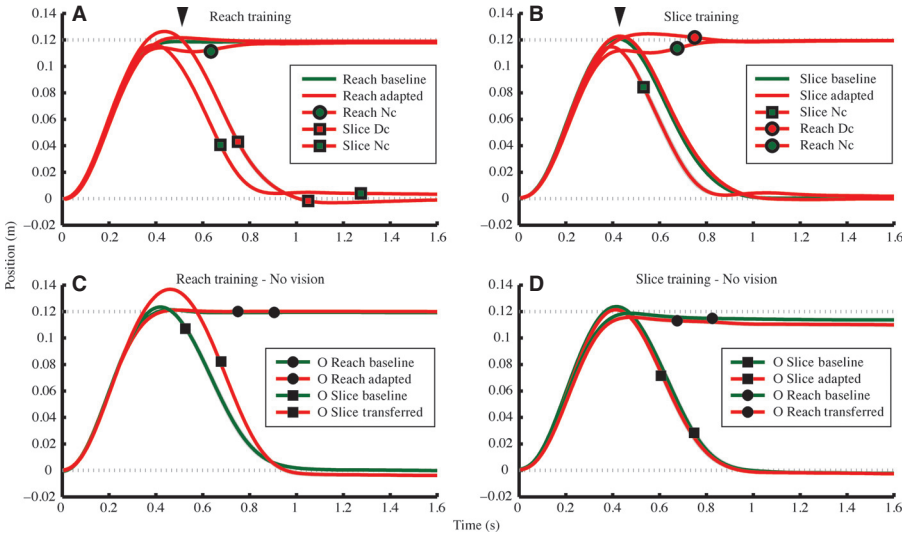


FIG. 6. Group mean trajectories showing hypermetria during omitted reach and transfer to slice (C), but not vice versa (D). Curve colors and symbols as in Fig. 5. The adaptation is evident here by comparing the similar extent of the trajectories between the baseline and the adapted state (A and B, green curves vs. red curves without symbols) and also by observing the undershoot extent during the zero-delay catch trial post-adaptation curve (A, green curve vs. red curve with green circle; B, green curve vs. red curve with green square). The black arrows mark the time when we tested whether adaptation took place by comparing the movement extent during zero-delay conditions before and after adaptation (A, green curve vs. red curve with green circle; B, green curve vs. red curve with green square). The omitted vision trials (C and D) are similar to our predictions in Table IV.

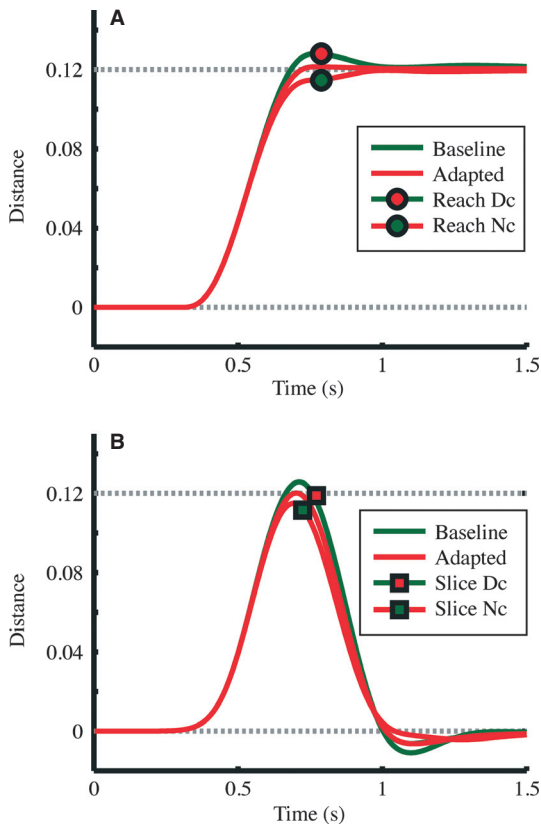


FIG. 8. Simulated reach and slice trajectories. Reaching (A) and slicing (B) vision trial trajectories before and after adaptation and during catch trials. The resulting trajectories replicate the basic observations of overshoot, learning, and undershoot observed in the behavioral data.

tion). In both groups, the transferred movements showed a statistically significant undershoot effect ($F_{1,4} = 7, P = 0.05, 4 \pm 1.5$ mm, and $F_{1,4} = 270, P < 0.001, 10 \pm 0.6$ mm for reach and slice training groups, respectively). These differences can be observed visually by inspecting the maximum extent of the post-transferred movements (Figs 5A and B, Figs 6A and B, green square and green circle, respectively) relative to the desired extent of the movement (dotted horizontal line at 0.12 m).

These results suggest that subjects can also adapt to the delay during the modified experimental protocol, but more importantly that reach and slice movements share at least some similar motor control mechanisms, which adapt as a result of the visuomotor delay perturbation.

Vision-omitted trials reveal different adaptations between movement types

In some pseudo-randomly chosen trials, prior to and after the adaptation block, subjects performed vision-omitted trials in both movement types (see Materials and methods; Fig. 2CII and III). To assess the effect of delay on omitted movements, we compared the maximum movement extent. We used a two-way ANOVA with repeated measures. The fixed factors were movement type (slice, reach) and adaptation (pre-adaptation, post-adaptation). We analysed the trajectories of each training group separately and also included an interaction factor in the model.

We observed a statistically significant effect of movement type in the 'slice-adapted' group: the overshoot of slice was just slightly more than the reach ($F_{1,12} = 5.23, P = 0.041, 5 \pm 2$ mm), whereas one was slightly overshooting the desired trajectory extent and the other undershooting it. Importantly, we did not observe any effect of adaptation on either one of the movements, nor did we observe any interaction effect between movement type and adaptation on movement extent. The accurate performance in the 'slice-adapted' group during omitted movements (Fig. 6D, green vs. red curves) indicates that there is no remapping of proprioception during adaptation to delay. In contrast, in the reach-adapted group (Fig. 6C), we observed a statistically significant interaction effect between adaptation and movement ($F_{1,12} = 13.4, P = 0.003$). A post-hoc paired t-test analysis (with Tukey correction for multiple comparisons) showed that, whereas reach omitted movements were not affected by the adaptation to delay ($T_{12} = -0.09879, P > 0.999$), slice omitted vision transferred movements were affected by the adaptation ($T_{12} = 5.95900, P < 0.001$), resulting in hypermetric movements (14 ± 2 mm).

These results imply that, following delay adaptation and during the vision-omitted condition, the transferred trajectories generalised asymmetrically between movement types, i.e. transferred slice movements overshoot the target exhibiting hypermetric trajectories (Fig. 6C, square curves), whereas transferred reaches did not change from their baseline condition (Fig. 6D, circle curves). The observed

TABLE 2. Mean lag between adapted and zero-delay slices

Group	Subject	Mean (ms)	95% confidence intervals (ms)
Slice adaptation	1	90	[65,111]
	2	73	[55,95]
	3	64	[38,91]
	4	104	[61,152]
	5	177	[117,267]
Reach adaptation	6	68	[94,125]
	7	43	[43,71]
	8	62	[62,108]
	9	67	[67,111]
	10	54	[54,89]
Average		80	[65,122]

hypermetric trajectories during transfer to slicing movements were consistent across all the subjects in the trained slice group, whereas during reaching movements, some subjects over-reached or under-reached slightly, with a group mean profile similar to that of the pre-trained condition. Taken together, the findings show that unbiased omitted reach disproves proprioception remapping, whereas the asymmetric transfer disproves a sole feedforward adaptation mechanism as we did not observe consistent undershoot movements during omitted post-adapted reaching trials, as is predicted by the feedforward single adapted hypothesis.

The neural controller should include a feedback forward-based model

Figure 3 illustrates a simple model that can account for our findings. We suggest that, during exposure to visuomotor delay, the forward vision model adapts to delayed visual feedback, such that after sufficient training, the delayed state is predicted accurately and, as a result, the prediction error diminishes to zero. During post-adaptation zero-delay catch trials with vision, the system uses its forward estimator as before, although this time the visual feedback state is not delayed. Thus, there is again inconsistency between the true state of the hand and the estimated state of the forward model, but in this case the forward model prediction lags behind the feedback state by the delayed duration of 70 ms, as if the hand is moving too rapidly. This will result in an on-line correction movement in the opposing direction that will drive the plant to the position set by the forward state prediction. The forward model will not respond immediately as it requires about 150 ms for the early afferent state to propagate back; only then can it be compared with the forward model output. Any prediction error will require a similar time until it starts to modify the hand trajectory. Therefore, we should expect a change in the trajectory only after 300 ms or later, similar to the observation during force perturbation. Wagner & Smith (2008) suggested 350–400 ms as the optimal time for the state prediction to become accurate once again. We used this idea and sought the time lag that would best explain the after-effect trajectory by first removing the initial movement phase up to the mean average time (370 ms) from each movement condition and then correlating between the two signals. We inspected this relationship for each adaptation group differently. For both groups, we used a similar method of correlation with 7 ms resolution between slice movements during two different conditions and analysed the results using the bootstrap method. For the slice adaptation group, we compared the adapted movement and the zero-delay catch trials post-adaptation (i.e. the trajectory averages presented in Fig. 6B, red vs. green

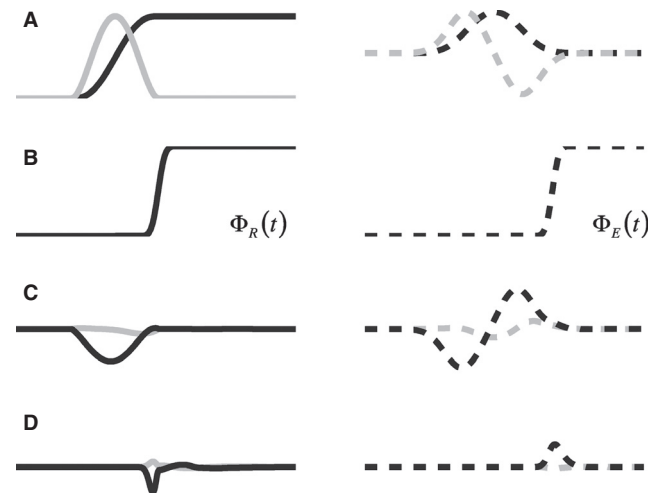


FIG. 7. The simulated movements for reach (solid lines) and slice (dashed lines) without delay. (A) The kinematics of the movements: hand displacement (black) and hand velocity (gray). (B) The posture trajectory gain (switching mechanism) for reach [$\Phi_R(t)$] and slice [$\Phi_E(t)$] before adaptation. (C) Feedforward shoulder torques (gray) and feedforward elbow torques (black). (D) The contributions of the reflex torques opposing the torques associated with the movement (colors as in C).

square curves). For the reach adaptation group, we compared the adapted catch movement with and without delay (i.e. the trajectory averages presented in Fig. 6A, red square vs. green square curves). Table 2 summarises these results showing that, in almost all cases, the mean lag with its confidence interval includes the 70 ms delay, except in one case where it is slightly higher. As in our model this movement error is related to the contribution of the forward model, this suggests that the after-effect movement is best described by a forward model that lags 80 ms around the post-adaptation trajectory, a value that almost exactly matches the artificially imposed delay of 70 ms. We address this issue again in the last section of the computational model that we present next.

Modeling

The observed effects of visuomotor delay on movement, together with the transfer between movements during vision trials and partial transfer during the omitted trials are difficult to explain by the existence of a simple control model having a single control mechanism. Instead, our computational model includes three basic components: feedforward, feedback, and reflex control modules. We assumed that the feedforward transforms desired trajectories into joint angles using inverse kinematics from which inverse dynamics is used to plan a motor torque command to the joints. The feedback uses vision and proprioception loops for on-line correction and for adapting its forward models, whereas the reflex loop enables stabilisation at the desired end-point.

We initially verified the model behavior by looking at the kinematics and dynamics during reach and slice movements. Movement time for reach and slice movements was selected manually to fit the baseline average group trajectory measured in the second experiment. Reaching movement was modeled using a minimum jerk model with a movement time of 470 ms, whereas slice movement was modeled using combinations of out-and-back reach movement, as in Scheidt & Ghez (2007) with a movement time of 1000 ms. These trajectories resulted in feedforward torques that were higher at the elbow than at the shoulder and also reflex tor-

ques, which were active at the stabilisation phase of the movement (see Fig. 7).

We first evaluated the performance of the system without a stabilisation controller in order to validate its contributions to our model. Figure 8A and B shows that, although the basic phenomena of overshoot and undershoot are simulated successfully for reach and slice movements, respectively, the end of the movements include minor oscillations. These oscillations were more obvious in the slice than in the reach and differed from the behavioral data. When the stabilisation/reflex controller is added, these oscillations diminish (Fig. 8A and B), thus justifying the addition of a posture controller to the model.

As in the model presented by Scheidt & Ghez (2007), ours includes a switching mechanism that initiates the stabilisation controller, which we model as a sigmoid function of time (see Fig. 7B). Slice and reach movements are modeled using two different switching functions: $\Phi_R(t)$ and $\Phi_E(t)$ respectively. Switching time is defined as the time when the sigmoid function is equal to 0.5 and was set at the time of peak jerk as calculated from the feedforward kinematics for each movement type. The resulting trajectories (Fig. 8C and D) replicate the basic observation of overshoot, learning, and undershoot observed in the behavioral data.

We next attempted to evaluate which of the model parameters might explain the asymmetric transfer of movement extent during vision-omitted trials. We would expect symmetric and accurate transfer between slice to reach movements and vice versa if the adaption occurs only in the vision feedback loop. However, as our behavioral data suggested otherwise, we further evaluated which of the feedforward properties could have contributed to the observed hypermetric slices. Using a similar approach to Scheidt & Ghez (2007), we investigated whether an error in issuing a wrong motor program that includes postural forces at the reversal point of a slice movement could explain our findings. Our simulation showed that slices became hypermetric when the slice feedforward command differed from its baseline condition in two aspects: when the postural control $\Phi_R(t)$ was activated in the outgoing phase of the slice movement when there was actually no need to initiate one, and when its switching time was earlier than the reaching baseline condition. When these two conditions were met, the slice trajectory became hypermetric during post-adaptation vision-omitted trials, but not during the vision-omitted reach condition (Fig. 9A). The range of initiation time that resulted in hypermetric movement was 70–120 ms (see Fig. 9B). This can be explained by the extra torques calculated in the feedforward controller that are required to overcome the hypothetical stabilisation forces at the reversal point, although these do not actually exist during the motion. These extra torques then drive the hand further than the required end-point location. For that reason, when these additional torques are initiated earlier while the hand is still in the outgoing phase, the trajectories become hypermetric in the outgoing movement.

When initiation time was identical to the reach baseline condition, the movement trajectory was not hypermetric in the outgoing movement, but rather in the back movement. This is due to a later initiation of the feedforward torques; hence, the trajectory did not overshoot the desired end-point, but instead overshoot the back movement as a result of the theoretical torques that were supposed to stabilise the hand at the reversal point (see Fig. 9B, dashed gray curve).

Discussion

In this study, we conducted two experiments to determine the effects of visuomotor delay on goal-directed movements. In the first

experiment (Fig. 4), we showed that, during unexpected visuomotor delay, the subject's hand trajectory overshoot the end-point but, during prolonged exposure to delay, the hand trajectory was adapted and returned to the baseline condition. When the delay was abruptly removed, the hand trajectory exhibited after-effects in the form of undershoot. In a second experiment, we inspected the transfer properties between two movement types, each with or without vision (Figs 5 and 6), and found that reach and slice movements share at least some similar controlling mechanisms, which adapted as a result of the visuomotor delay perturbation. We also concluded that the neural controller should include feedback adaptation as well as transfer to feedforward adaptation. In the light of our results, we present a computational model (Fig. 3) that includes a pair of feedback and feedforward controllers accounting for these findings (Fig. 8). This model unifies two existing models: the feedback control portion is similar to the model of Wagner & Smith (2008) and the stabilisation and trajectory controller is similar to that of Scheidt & Ghez (2007).

The effects of visuomotor delay on movements have been previously investigated, but mostly in continuous and complex motor tasks such as tracking (Miall *et al.*, 1993; Langenberg *et al.*, 1998; Foulkes & Miall, 2000), target avoidance (Cunningham *et al.*, 2001a), and hitting, or during complex daily tasks such as driving (Cunningham *et al.*, 2001b), but never in reaching movements.

Unlike reaching movements, complex movements include a wide range of elementary synchronised movements superimposed with corrective movements. Therefore, the methodology of complex tasks makes it difficult to distinguish between corrective movements that result from the complex task *per se* and corrective movements that result from error in performance due to the delay. One exception has been shown in a study by Smith & Bowen (1980) that explored the effects of visuomotor delay during simple reaching movements, comparing it with the effects of visual wedge prisms. In this study, it was found that introducing visuomotor delay caused overshoot of reaching movements, which diminished to baseline after practice and that, upon removal of the delay, there was an after-effect in the form of undershoot. In this work, the authors did not provide an explanation for these observations.

The technology used in these earlier experiments was based on video recording and delayed video playback, whereas the hand displacements were recorded using a pencil and paper. This method might have been novel at the time and suitable for observing fundamental effects, but it was not sufficient to experimentally control and facilitate observation of other features of movement such as movement velocity. More importantly, these experiments were conducted before the introduction of concepts of motor control such as forward models and inverse models (Kawato *et al.*, 1987; Jordan & Rumelhart, 1992; Kawato & Gomi, 1992; Binder, 2009), and thus, the observations were not made in the light of these concepts. At that time, it was therefore concluded that adaptation was a result of "fore-shortening the efferent movement command" (Bowen, 1976). Our current results challenge this conclusion and suggest an alternative explanation based on the concept of model-based feedback adaptation and the utilisation of an inverse forward model in the feedforward controller.

An important result of our study is the reported overshoot observed during vision-omitted rapid reversal movements following delayed reaching adaptation (Fig. 6B). These findings are in agreement with those of Scheidt & Ghez (2007), who compared adaptation to reach and transfer to slice during visuomotor rotation. Previous work on the accuracy of repetitive slicing movements during vision-omitted conditions (without visuomotor delay pertur-

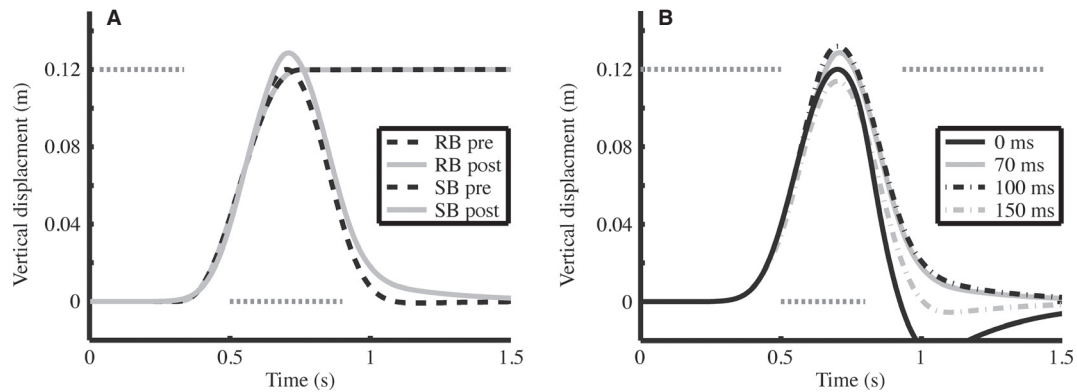


FIG. 9. Modeling the asymmetric transfer during vision-omitted trials. (A) Reach and slice blind trajectories (RB and SB, respectively) pre-adaptation (dashed black lines) and post-adaptation (gray lines). The adapted slice vision blind trajectory is hypermetric, unlike the reach movements, which are identical. The SB post-trajectory was modeled by adding a posture point $\Phi R(t)$ during slice at a time that is 70 ms earlier than in the RB pre-condition. (B) Effect of switching times on SB post-adaptation trajectory; different posture point timing (relative to the RB pre-condition) leads to different trajectories. Similar switching time to the RB pre-condition (0 ms) leads to hypermetric trajectory only at the final home position and not in the outgoing movement.

bation) reported that these repetitive movements may lead to deviation from the initial hand position, although the extent of the movement path (amplitude) was not affected (Brown *et al.*, 2003a,b). These findings were explained in terms of the ability of the motor system to accurately recalculate the inverse dynamics even though different starting positions were used. In contrast, our results showed that, during visuomotor delay, the transferred omitted slicing movements were hypermetric, suggesting, by the same rationale, that the inverse dynamics had changed. Our model proposes that this change is the result of the feedback–feedforward inverse relationship, previously suggested by Jordan & Rumelhart (1992) and used to explain adaptation to force perturbation (Bhushan & Shadmehr, 1999; Wagner & Smith, 2008).

The computational model that we present here includes internal forward models. Prediction mechanisms utilising forward models have been used previously to explain grip force generation (Flanagan & Wing, 1997) and adaptation to visuomotor rotation (Mazzoni & Krakauer, 2006). Our results extend the topology of this model to adaptation to altered sensory delays. The use of an internal forward model is often justified in order to overcome sensory delays, but internal forward models have not been previously used to explain adaptation to altered delay *per se*.

This raises the question of how delay is compensated. Here, we propose two possible mechanisms. The first option includes a dedicated component in series with the forward model that is responsible for delay compensation. This can be either a Smith predictor (Miall *et al.*, 1993) or another forward model by itself that adapts purely according to temporal errors. The second option is that the forward model simply adjusts according to the errors, the learning rules, and learning gains, without distinguishing between state error arising from space-state or from unexpected delays. The former has the advantage that, once delay is calibrated, it can be used for the entire repertoire of movements. However, this requires the use of an additional system that needs to have adaptation capability as well as a mechanism to separate between state-driven and delay-driven errors. Our results with hypermetric slices suggest that transfer was incomplete and that the delay was not learned independently but rather as part of the broader forward model. Therefore, during perturbed delay catch trials, the forward model does not accurately predict the feedback state, which results in incorrect motor commands in the form of overshoot or undershoot during opposing delay (Dc) and zero-delay (Nc) trials, respectively.

The correlation analysis that we present suggests that, following adaptation, the forward state adapts in order to compensate for the imposed visuomotor delay, whereas the computational model suggests that a feedforward switching mechanism learned an earlier state. Altogether these results are consistent with joint feedback and feedforward controllers adapting concurrently.

Our model unifies several reported motor control properties, such as on-line feedback control, two separate feedforward controllers, and two independent feedback loops. On-line feedback control was previously suggested as an explanation for movement corrections within a reaching movement during various feedback manipulations (Prablanc & Marti, 1992; Saunders & Knill, 2003; Saunders and Knill, 2005; Ma-Wyatt & McKee, 2007; Shabbott & Sainburg, 2009). Our results extend this observation to include adaptation to visuomotor delay. The concept of two parallel feedforward controllers, one for the end-point and the other for trajectory planning, is also consistent with previous studies that show: (i) separate processes for trajectory and end-point movements in normal subjects (Sainburg & Wang, 2002; Wang & Sainburg, 2005; Arce *et al.*, 2009; Scheidt *et al.*, 2011) and (ii) stroke-region-specific damage and its effects on these variables (Haaland *et al.*, 2004; Schaefer *et al.*, 2007, 2009) during exposure to Coriolis force fields (Dizio & Lackner, 1995; DiZio & Lackner, 2001) or during generalisation from the dominant to the non-dominant hand (Duff & Sainburg, 2007). The ability of blind subjects to adapt to perturbations (DiZio & Lackner, 2000; Gosselin-Kessiby *et al.*, 2009) or a similar adaptation capability of subjects with a proprioception feedback deficit (Bernier *et al.*, 2006) suggests that each modality has the ability to adapt independently of the other. In addition to the obvious benefit of redundancy in the living organism, this lack of dependence provides two additional benefits. First, it impedes the need for the transformation of motor errors from a vision-extrinsic coordinate to a motor-intrinsic one (Ghez *et al.*, 2007) during on-line correction where processing delays are required to be as minimal as possible. Second, it offers the ability to update either the trajectory or the end-point feedforward controller independently, thus providing a means to independently account for trajectory or posture control. As a whole, this model is also consistent with the ability of the brain to predict the hand state during reaching movements (Ariff *et al.*, 2002), with recent findings claiming that an on-line feedback mechanism compensates for the sensory delays (Gritsenko *et al.*, 2009), and with functional magnetic resonance imaging findings showing

differences in activation patterns during discrete and rhythmic single wrist movements (Schaal *et al.*, 2004).

The notion that the forward model may contribute to incorrect correction movements has been presented previously (Bhushan & Shadmehr, 1999), and we suggest that this is also the phenomenon observed in our study. During repetitive and continuous exposure to delay, the forward model learns the delayed state, and the inverse model adjusts accordingly, as would be expected from coupled controllers (Wolpert & Kawato, 1998). The ability to adapt to delays was previously reported during grip force manipulation and explained by the existence of forward models (Witney *et al.*, 1999).

It has also been shown that visual spatial errors are accounted for during reaching movements (Saunders & Knill, 2003). However, spatial errors differ from temporal displacement in two basic ways. First, temporal displacement during a bell-shaped velocity profile (Flash & Hogan, 1985) generates a non-constant spatial shift. Second, during temporal perturbation, subjects can reach accurately by ignoring the visual feedback, which is not the case with spatial displacements. Theoretically, visual delayed feedback can be compensated by scaling the weights of vision and proprioception in Bayesian integration formalism (Ernst & Banks, 2002; Kording *et al.*, 2004). However, if adaptation were achieved through this scaling mechanism, one would have expected that, during delayed visual feedback, the proprioceptive feedback would have dominance over the distorted visual feedback. The observed undershoot during non-delayed catch trials suggests that visual feedback dominance was not diminished, at least not entirely. Further experiments with reaching movements during visuomotor delay, together with measurement of internal state estimate during the experiment, may resolve this question.

The two experiments that we conducted differed in methodology. In one experiment, the robot return was passive, whereas in the other, it was active. Another difference was in the time it took the target to appear following stabilisation in the home position. A third factor affecting this study is the group size, which was relatively small. Hence, further experiments are required to validate that these conditions did not contribute to the observed effects. In addition, future experiments are required in order to re-examine the main attributes of motor learning for this context such as spatial generalisation and retention of adaptation.

The importance of our observations extends beyond the scope of delayed visuomotor reaching or slicing and may explain how feedforward control, proprioception feedback control, and vision feedback control are joined together during movements and motor learning. In addition, our model provides a possible explanation for the compensation mechanism in response to abrupt or gradual changes in afferent and efferent delays.

A final point we have addressed is the similarities and differences between the visuomotor delay paradigm and others, such as the visuomotor rotation and the force perturbation paradigms. In contrast to the visuomotor rotation paradigm, during point-to-point reaching movements with force perturbation or visuomotor delay, the start and end-point spatial positions remained the same and the adapted trajectory state was similar to the baseline condition. Unlike adaptation to force fields where joint torques must change in order to overcome the force field, the visuomotor rotation and visuomotor delay paradigms also share some similarities by not changing those properties in order to elicit adaptation. Thus, visuomotor delay shares some properties with each of the above well-known paradigms. Hence, we suggest that visuomotor delay can be used in a similar way to assess changes in the motor system after adaptation to reach-

ing movements in a variety of experimental setups or for enhancing errors during robot-assisted rehabilitation (Patton *et al.*, 2006).

Understanding how the brain compensates for neural conduction and processing could provide insight into the motor control mechanisms and also be useful for future development of human/machine interfaces, such as prosthetic arms (Hochberg *et al.*, 2006; Velliste *et al.*, 2008) and visual prostheses (Schmidt *et al.*, 1996; Zrenner, 2002).

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Abbreviations

D, delayed; Dc, delayed catch trials during non-delayed block; N, non-delayed; Nc, non-delayed catch trials during delayed block.

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