Integration of Predictive Feedforward and Sensory Feedback Signals for Online Control of Visually Guided Movement

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Gritsenko V, Yakovenko S, Kalaska JF. Integration of predictive feedforward and sensory feedback signals for online control of visually guided movement. J Neurophysiol 102: 914–930, 2009. First published May 27, 2009; doi:10.1152/jn.91324.2008. Online control of movement requires complex integration of predictive central feedforward and peripheral sensory feedback signals. We studied the hand trajectories of human subjects pointing to visual targets that abruptly changed locations by different amounts and modeled the mechanism of rapid online correction using a dynamic model of a two-joint limb. Small unperceived and large detected target displacements could be attributed to different origins (motor execution errors vs. environmental changes, respectively) and compensated differently. However, the behavioral findings indicate that the rapid feedback pathway is recruited regardless of the amplitude or subjective awareness of target displacement and that the size of the earliest correction is always proportional to the amplitude of the target displacement over the tested range of perturbations. The modeling findings suggest that the rapid online corrections can be accomplished by superimposing a dynamically appropriate error correction signal onto the outgoing feedforward motor command to the original target. Furthermore, the modeling shows that the online correction mechanism must include compensation for the dynamic mechanical properties of the limb and for sensory delays in its error-correction pathway.

INTRODUCTION

The central goal of this study is to investigate the mechanisms of the online control of human reaching movements. One behavior that has provided a number of insights into the organization of online motor control is the rapid initial adjustment of reach trajectories that occur in response to abrupt changes in target location immediately before or just after the onset of the reach (Day and Brown 2001; Day and Lyon 2000; Desmurget et al. 1999; Pelisson et al. 1986; Pisella et al. 2000; Prablanc and Martin 1992). The short-latency corrective responses occur even when subjects are unaware of the target displacement (Johnson and Haggard 2005; Pelisson et al. 1986; Pisella et al. 2000; Turrell et al. 1998) and are relatively resistant to cognitive control (Castiello et al. 1991; Cressman et al. 2004; Day and Lyon 2000; Pisella et al. 2000; Rodriguez-Fornells et al. 2002), which suggests that it is an “automatic” correction process as distinct from a willful “voluntary” correction. The short latency of trajectory correction suggests that its mechanism involves a predictive efferent copy-based state estimation process such as an internal forward model of future limb states (Cooke and Diggles 1984; Higgins and Angel 1970; Jaeger et al. 1979; Wolpert et al. 1995). Transcranial magnetic stimulation (TMS) studies in neurologically normal subjects and behavioral studies in optic ataxic patients have implicated the parietal lobe in this automatic correction mechanism (Battaglia-Mayer et al. 2001; Della-Maggiore et al. 2004; Desmurget et al. 1999; Pisella et al. 2000; Rossetti et al. 2003; Tunik et al. 2005; van Donkelaar et al. 2000).

This study focuses on two different aspects of the rapid online correction mechanism that have not been studied in detail before. The first is how well the kinematics of the rapid corrective response to an unpredictable change in the direction of the target from the starting location scales with the size of the directional change. The second concerns whether the corrective signal can be purely kinematic in nature or must instead take into account the dynamics of the limb. To address the first question, we did a psychophysical study of reach trajectory corrections in human subjects in response to target displacements. To address the second question, we did a modeling study to assess the ability of control circuits with different computational architectures to replicate the reach trajectory kinematics observed in the human behavioral study.

No study to date has documented how closely the size of the trajectory corrections scale with the amplitude of target direction changes at different times after the target displacement. The scaling of trajectory corrections addresses the issue of credit assignment in motor control, i.e., to what degree the motor system attributes the origin of a sensed reaching error to internal causes because of the subject’s own motor system or to external causes because of events in the world (Berniker and Kording 2008; Kluzik et al. 2008; Malfait and Ostiry 2004; Wei and Kording 2009). It is possible, for instance, that the main function of the rapid automatic online correction mechanism is to correct for small performance errors that result from stochastic variability in the planning and execution of movements (“motor noise”); Gordon et al. 1995; Kording and Wolpert 2006; Messier and Kalaska 1999; Stein et al. 2005; van Beers et al. 2004; Wolpert et al. 1995). As a result, there may be a maximum limit to the size of the trajectory correction that could be mediated by the rapid correction mechanism, beyond which the rapid corrective response would saturate. In contrast, the motor system might attribute large performance errors to an unexpected change in the environment and compensate for them primarily by activation of a different corrective pathway, including longer-latency overt “voluntary” changes in motor output commands (Kluzik et al. 2008; Wei and Kording 2009). The hypothesized credit assignment dichotomy might result in a two-stage correction for large target displacements, involving an early partial correction mediated by the saturated rapid online correction mechanism, followed by a delayed “voluntary” correction to compensate for the remainder of the displacement. This two-stage process would result in a sigmoidal
relationship between target displacement size in opposite directions and the size of corrective trajectory deviations early in the movement, which changes to a more linear relationship later in the movement. Alternatively, the rapid online correction mechanism might not be activated by a large target displacement, resulting in only a delayed correction at the usual voluntary visual reaction time.

This potential distinction is supported indirectly by differences in learning, retention and generalization of adaptation to perturbations that the motor system might attribute to internal versus external origins, such as perturbations that are introduced gradually and imperceptibly in small incremental steps versus abruptly in one large step (Ingram et al. 2000; Kagerer et al. 1997; Kluzik et al. 2008; Malfait and Osty 2004) or that are in intrinsic versus extrinsic reference frames (Berniker and Kording 2008). Similarly, Wei and Kording (2009) showed that subjects made approximately linear trial-to-trial adaptive changes to reaching movements when they introduced small perturbations in the visual feedback of final hand position, but that the adaptive response became significantly nonlinear (saturated) for large feedback perturbations. This suggested that the motor system tended to attribute small perturbations to its own performance and attempted to adapt to the sensed error but tended to discount large frequent perturbations as caused by an unpredictable external origin and therefore irrelevant (Wei and Kording 2009).

We examined whether the rapid online correction of reaching errors showed evidence of a similar two-stage credit-assignment process by studying trajectory corrections evoked by target displacements that produced a larger range of directional errors than used in most studies of automatic online corrections. We also assessed whether any possible transition point in the kinematics of corrective responses, i.e., nonlinear scaling of trajectory corrections with the amplitude of target displacements, might be coupled to the presence or absence of awareness of the occurrence of the target displacement.

In addition to studying the extent to which the rapid feedback pathway can compensate for visuomotor errors of different sizes, in a separate experiment, we used computational modeling to investigate the nature of the corrective signal responsible for this compensation. The objective of this modeling study was not to explain the findings of the behavioral study for small versus large target displacements but rather to assess the ability of different computational architectures to produce the general patterns of trajectory corrections. The idea that the neural control of limb movements encompasses both feedforward motor commands and sensory feedback components has been around since before the turn of the 20th century (Mott and Sherrington 1895; Woodworth 1899). Nevertheless, how these components are integrated to produce a motor command to the muscles that results in an accurate movement of the limb to a desired goal are still being intensely debated (Bhushan and Shadmehr 1999; Desmurget and Grafton 2000; Todorov and Jordan 2002; Wolpert and Kawato 1998). Recent experimental findings indicate that the hand trajectory corrections result from two overlapping signals: the feedforward motor command to the original target, which is available before the start of movement, and an error-corrective signal that takes into account any changes in the target position after the start of movement. This is supported by evidence that the online correction can be selectively suppressed without interfering with the movement to the original target location (Desmurget et al. 1999; Pisella et al. 2000). Computational studies have further explored the organization of online control of arm movement by showing that the corrective signal can be computed based on the kinematic difference between the continuous estimates of target and limb states based on afferent and efferent signals (Flash and Henis 1991; Henis and Flash 1995; Hoff and Arbib 1993; Nijhof 2003).

Moreover, other studies argue for the importance of an internal model that compensates for the complex dynamics of a multisegment limb (Desmurget and Grafton 2003; Sabes 2000; Wolpert and Kawato 1998). Furthermore, several studies suggest that a common internal model may be used to compensate for limb dynamics during both planning and execution of movement (Kurtzer et al. 2008; Lacquaniti and Soechting 1984; Soechting and Lacquaniti 1988; Wagner and Smith 2008).

However, no study has addressed the question of what is the simplest necessary error correction signal for successful online corrections for target displacements during reaching. For example, if the feedforward motor command to the original target compensates for limb dynamics, a simple correction signal proportional to the kinematic hand-to-target direction error might be sufficient to deviate the reach trajectory toward the new target location. This is made more plausible because the requisite trajectory corrections in most studies of rapid online control are usually fairly small. Furthermore, similar combinations of a feedforward motor command and kinematic error feedback is an effective and common way to control robotic devices in engineering (Braunl 2003; Goodwin and Sin 1984). In most robotic devices, the discrepancy between the desired and actual robot position (kinematic error) is simply scaled by a constant (gain) and added to the outgoing (feedforward) torque signal. We tested the feasibility of a physiologically plausible model that includes a feedforward/feedback controller and a multisegment arm with complex, nonlinear dynamic properties to reproduce the online correction performance observed in humans.

METHODS

Task apparatus

The task apparatus consisted of a digitizing tablet to capture reach trajectories, an oculometer to detect onset of ocular saccades, and a suspended LCD monitor to display visual targets on a semisilvered mirror mounted horizontally between the subjects’ eyes and their hand (Fig. 1A). The digitizing tablet (GTCO CalComp, Columbia, MD; 0.915 × 0.608 m; spatial resolution, 0.006 ± 0.127 mm) captured the movement of a stylus that the subjects held in their hand, over the surface of the tablet at 100 Hz. Both the stylus and the subject’s arm were visible through the semitransparent mirror at all times. The monitor displayed visual targets 7 mm in diameter, which reflected from the mirror and appeared to be on the surface of the tablet in the plane of the subject’s hand movements. Images on the monitor were produced by a Visual Stimulus Generator (VSG, Cambridge Research Systems, Rochester, UK) PC card, which was programmed using Matlab 7 (The Mathworks, Natick, MA) software. Eye movements were captured using a Skalar IRIS IR oculometer (Cambridge Research Systems) and sampled at 2 KHz by the VSG card. Both hand and eye movements were synchronized using the VSG internal clock and recorded for analysis offline.

Behavioral task

Eight right-handed human subjects (3 women, 5 men; mean age, 27 yr) with no known neurological deficits and normal or corrected to normal visual acuity participated in the study. They all gave informed consent before their inclusion and were naive to the objectives of the
The study was approved by the Human Research Ethics Committee of the Faculté de Médecine, Université de Montréal, and was carried out in accordance with the ethical standards set by the Committee.

The experiment consisted of two data collection sessions on separate days. During the sessions each subject performed five sets of 64 trials per day separated by short breaks, for a total of 320 trials per daily session and 640 trials per subject for the two sessions. Each trial started with the subject placing the tablet stylus and fixating his/her gaze on a visual target displayed on the surface of the tablet along the midline of their visual field (T0; Fig. 1B). After a 2-s delay, T0 disappeared and a new target appeared in one of the two locations in the right visual hemifield at a 30° (T1^30) or 60° (T1^60) angle to the horizontal axis (x-axis; Fig. 1B). Both T1 locations were 15 cm away from the initial position, which corresponded to a 15° visual angle. The subjects were instructed to look at the T1 target and simultaneously move the stylus to it as quickly and accurately as they could, by making a reaching movement in the plane of the tablet. In the beginning of the first session, subjects performed 20 practice trials without target jumps to familiarize themselves with the task.

In one half of the trials, the T1 target changed its location before the middle of the ocular saccade (jump trials). Saccade onsets were detected online from the oculometer signal with a velocity threshold algorithm. The algorithm determined when the eye-movement velocity

FIG. 1. Experimental paradigm and methodology. A: schematic of the experimental setup. B: coordinate system and target locations relative to the subject: T0, starting location, T1^30 and T1^60, initial target locations 30 and 60° away from the x axis; T2^14, example of a jumped target location showing a 14° jump clockwise relative to the T1 direction. C: timeline of events during a typical trial. Thick gray lines indicate times of target appearances, solid black lines show times of hand-movement related events, and dashed black lines indicate times of eye movement–related events. D and E: illustration of the method to detect the onset of on-line correction. Thin arrows in D shows how the instantaneous trajectory angle was calculated. Solid line indicates control trajectory; dashed line indicates trajectory with a target jump. The calculated instantaneous trajectory angle is plotted in E for both trajectories, together with the difference between the 2 (thin solid line). The width of the gray box represents the time period used to estimate baseline variability in the difference trace; the height of the box shows the 95% CI used to detect the onset of on-line correction, defined as the 1st value outside the CI. F and G: functions fitted to the relationship between the target jump amplitude and the tangential angle of trajectories. Absolute tangential angles were used for fitting a quadratic function in G.
ity exceeded 5% of the mean peak saccade velocity, which was determined from the baseline recordings done during the practice trials. The target changed position on the screen between 5 and 17 ms after the saccade onset detection. The target jumped to one of eight locations along the arc of 15 cm radius with angular increments of 3.5° (T2±1.5°), 7° (T2±2°), 10.5° (T2±3.5°), and 14° (T2±4°), where the positive direction of target jumps was counterclockwise (Fig. 1B). These angular displacements relative to the original T1 direction corresponded to visual angle changes from 1 to 4°. The timeline of events in a typical trial is shown in Fig. 1C. Before performing the task, the subjects were told that the targets could change position in some trials, and at the end of each trial, subjects reported if they saw the target jump in that trial or not. The sequence of trials with and without jumps and the values of amplitude and direction of target jumps were presented in a randomized block design. Each block included a trial for each combination of T1 and T2 target displacement conditions (16 trials) and an equal number of control trials without target jumps (8 trials for each T1). Two blocks of 32 trials were repeated consecutively with randomly permuted trials within each condition (16 trials) and an equal number of control trials without the target jump in that trial or not. The sequence of trials with and without jumps, and the values of amplitude and direction of target jumps were presented in a randomized block design. Each block included a trial for each combination of T1 and T2 target displacement conditions (16 trials) and an equal number of control trials without target jumps (8 trials for each T1). Two blocks of 32 trials were repeated consecutively with rat-jump terminated trials per T2 target and 160 baseline no-jump trials per T1 target in total across the two daily sessions. The subjects could see the position of their hand at all times through the semisilvered mirror relative to the reflected image of the target locations.

Analysis

Data analysis was carried out offline using Matlab 7. The hand displacement traces were low-pass filtered at 20 Hz, and each trial was aligned to the onset of reaching movement, when hand velocity surpassed 0.05 m/s. The onset of online correction was determined using a method based on the difference between the mean target-jump trajectories and the mean baseline trajectory (without target jumps) for each subject in each condition (Fig. 1, D and E). First, tangential angle (α) of each trajectory was calculated using the formula α = arctan(Δy/Δx), where Δx and Δy are derivatives of the horizontal and vertical components of mean hand trajectory at each 10 ms time step (Fig. 1E). Second, the tangential angle of the baseline trajectory was subtracted from that of the target-jump trajectory. Third, the 95% CI was determined using a t-test of the baseline difference values in the first 100 ms after the start of movement before the earliest online correction is expected (Fig. 1E). Last, the onset of online correction was defined as the first value of the difference trace outside the CI after the initial 100-ms period. Additional constraint on onset detection was that the subsequent values of the angular difference trace had to be outside the confidence interval for ≥80 ms. This analysis was also performed on trajectories aligned to the time of target jump, and results were the same as those reported from trajectories aligned to the onset of movement (data not shown). Statistical analysis of trajectory correction onsets was performed using a repeated-measures ANOVA with two main factors, initial target location (2 levels) and signed target jump amplitude (8 levels) using SYSTAT 11 (SYSTAT Software, San Jose, CA). When the sphericity assumption of ANOVA was violated, the Greenhouse-Geisser correction was used to estimate the P value.

Ideally, one would like to be able to detect the onset of the trajectory corrections on a trial-to-trial basis. We initially attempted to use the correction-onset detection algorithm on single-trial basis. However, we found that the high variability of the moment-to-moment kinematic data for single trials reduced the sensitivity of the algorithm to detect the onset of a trajectory correction, yielding much longer onset times on average than those detected by the method described above and also considerable scatter of onset times within and across task conditions and subjects. Furthermore, the single-trial method was even less sensitive to small deviations during small target jumps than to larger deviations during larger target jumps because the smaller expected trajectory corrections were even more difficult to detect in the noisy data traces (data not shown). As a result, we chose to present the analyses based on the mean trajectories as an acceptable compromise.

To determine whether the amount of online correction was linearly related to the amplitude of the target jump, we used tangential angle values of hand trajectories. We fitted a linear regression between the tangential angles and the amplitude of the target jump at every 10-ms time step after hand movement onset. The linear function was \( y(x) = ax + c \), where \( y \) is the angle of trajectories with target jumps of different amplitudes taken at the same time after the onset of movement; \( x \) is the amplitude of the target jump; and \( a \) and \( b \) are constants. Furthermore, for data from individual subjects and the compound means a comparison was made between linear, quadratic, and sigmoidal fits to the tangential angles taken at two instances: when the hand reached peak velocity and when the hand decelerated to half of peak velocity. The sigmoidal function used was \( y(x) = a/(1 + e^{-bx}) + c \), where \( y \) and \( x \) are the same as described above; \( a \), \( b \), and \( c \) are constants; and \( e \) is exponent. The quadratic function used was \( y(x) = ax^2 + b \), where \( y \) is the absolute angle of trajectories with target jumps of different amplitudes taken at the same time after the onset of movement; \( x \) is the same as described above; \( a \) and \( b \) are constants. Fitting was accomplished with the least-squares method, and goodness of fit of the sigmoidal, quadratic, and linear functions was compared for corresponding time periods using \( R^2 \) values. A significantly better fit to a sigmoidal function would indicate that the size of the trajectory correction saturated for larger target displacements in the two opposite directions while scaling linearly with the size of smaller displacements in both directions (Fig. 1F). A significantly better fit to a quadratic function would indicate that trajectory corrections scaled nonlinearly with the amplitude of the target jumps (Fig. 1G).

Model

The model arm comprising two segments connected with two rotational joints was built using Simulink and SimMechanics toolboxes of Matlab (Fig. 2A). Segments were modeled as cylinders of 30 cm length, 3 cm radius, and 2.5 kg mass each (Winter 1990). The starting posture of the virtual arm corresponded to a 60° shoulder angle (relative to the horizontal x-axis) and a 120° elbow angle (relative to the previous segment; Fig. 2A). Viscous resistance of joints modeled the intrinsic velocity-dependent property of muscles acting around the joints. The value of viscosity \( B = 0.2 \text{ Nms/rad} \) was chosen within reported physiological values of 0.14 and 0.26 Nms/rad in human subjects (Bennett 1993; Selen et al. 2006).

The arm controller was modeled as the sum of a feedforward motor command and an online correction signal, where the correction signal with a constant gain (\( G \)) was superimposed on the feedforward command to move to the initial target T1. The online correction signal comprised a directional error between target location and current arm state. The purpose of this model was to infer the nature of the corrective signals for the online correction mechanism. Consequently, the model was not designed to study such phenomena as multisensory integration or the effect of noise and uncertainty in sensory signals or motor output commands. Therefore for simplicity, the model included two feedback signals: target location and arm state. The model assumed that they are accurate and they arrived at the central online correction circuitry at the minimal latencies reported in the literature. Also importantly, for the sake of simplicity, these feedback signals are “jumped” signals that are an amalgam of all possible sources of information about target location and arm state. For instance, the target position signal can include both accurate retinal feedback about changes in target position whether they are perceived or not, and further refinements of estimates of target location that can be calculated from different copies of the saccade motor command to the initial target location and any subsequent corrective saccades.
The feedforward motor program in the model consisted of joint torques ($\tau_{T1}^\text{f}; \text{Fig. 2B}$) necessary to move the endpoint of the virtual arm along the mean control trajectory of human subjects for baseline movements to the T1 target (Fig. 1D, solid line). Without target jumps, the feedforward motor program brought the model endpoint to the target within 390 ms after the start of movement, which was equal to the mean duration of the unperturbed reaching movements of the human subjects. We used the mean subject trajectory to one of the targets, T1$^{160}$, for constructing the feedforward movement to both T1 targets. This removed the confounding differences between feedforward trajectories to different targets and left only the differences between trajectories caused by error correction. To simulate baseline movements to the T1$^{160}$ target, the horizontal and vertical components of the endpoint trajectory toward the T1$^{160}$ target were scaled to end on the T1$^{130}$ target. However, all simulations were also repeated with the subject’s mean T1$^{90}$ trajectory with the same results. To generate feedforward joint torques, the endpoint trajectories for the two movement directions were recalculated into the appropriate joint kinematics followed by joint torques using the inverse dynamic model (IDM) of the limb in SimMechanics. The IDM included a virtual arm identical to the plant (Fig. 2, A and B), which it used to predict joint torques necessary to produce any desired movement.

We studied the performance of four controllers. The first two controllers (Kin1 and Kin2) included kinematic error correction (Fig. 2B, both switches a and b are in position 1). The torque $\tau_{T1}^\text{f}$ that was driving the dynamic model of the limb consisted of the following components

$$\tau_j = \tau_{T1}^\text{f}_j + G \cdot p_{err}^\text{f} - B \cdot \omega_j \quad (1)$$

where $j$ is joint index (elbow or shoulder); $\tau_{T1}^\text{f}_j$ is feedforward torque to the T1 target (main target before jump); $G$ is gain constant; $p_{err}^\text{f}$ is kinematic error in the joint-based coordinate system; $B$ is viscosity constant; and $\omega_j$ is joint angular velocity.

The correction signal in the Kin1 controller was proportional to the error between the desired and sensed endpoint trajectories, converted into the joint-based reference frame ($p_{err}^\text{f}$ in Fig. 2, B and C). The error in the joint-based coordinate system ($p_{err}^\text{f}$) was calculated from the endpoint error using a kinematic transformation in SimMechanics. The mediolateral ($p_{xerr}^\text{f}$) and antero-posterior ($p_{yerr}^\text{f}$) components of the endpoint error were calculated as follows

$$p_{xerr}^\text{f} = p(t - \gamma_x - \gamma_y) \cdot \left[ \cos[\theta_x(t - \gamma_x)] - \cos[\theta_{xep}(t - \gamma_x - \gamma_y)] \right] \quad (2)$$

$$p_{yerr}^\text{f} = p(t - \gamma_x - \gamma_y) \cdot \left[ \sin[\theta_x(t - \gamma_x)] - \sin[\theta_{xep}(t - \gamma_x - \gamma_y)] \right] \quad (3)$$

where $p$ is endpoint distance away from the starting position; $\gamma_x$ is descending delay; $\gamma_y$ is proprioceptive delay; $\theta_x$ is target angular position (angle of T1 or T2 target relative to horizontal); $\gamma_{xep}$ is visual delay; and $\theta_{xep}$ is endpoint angular position (angle of endpoint relative to horizontal).

The endpoint error vector pointed in the direction of the target jump with its amplitude proportional to the change in the direction of movement ($p_{err}^\text{f}$ in Fig. 2C). This type of error correction was inspired by the idea of vectorial control of movement, in which amplitude and direction are separately controlled variables (Gordon et al. 1994; Rossetti et al. 1995; Sarlegna et al. 2003).

The Kin2 controller included a kinematic error that was calculated as in Kin1 (Eqs. 2 and 3). However, instead of the delayed peripheral arm-state feedback used in Kin1, the correction in Kin2 relied on a centrally estimated arm state signal that led the actual movement by the value of $\gamma_x$. This simulated an internal prediction of sensed arm position $\gamma_x$ into the future by a forward dynamic model (FDM) based on the effference copy of the outgoing motor command (Fig. 2B, switch a is in position 2, switch b is in position 1). In theory, the FDM

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includes a model of the plant (Fig. 2, A and B), which it uses to predict movement that would result from any given torque. A practical implementation of this in our model is to set the delays to 0 (\( \gamma_d + \gamma_0 = 0 \) in the Eqs. 2 and 3), thus obtaining predicted arm state values for error correction.

The other two controllers, Dyn1 and Dyn2, were in essence the Kin1 and Kin2 controllers with the IDM added to their error correction pathways, which compensated for limb dynamics. For these controllers the driving torque \( \tau_j \) was

\[
\tau_j = \tau_{j1} + G_j \tau_{err} - B_j \omega_j \tag{4}
\]

where \( \tau_{err} \) is joint torque error calculated by IDM from \( \tau_{err} \) and its derivatives. The Dyn1 controller used the IDM to convert the delayed sensed kinematic error, calculated as in Kin1, into joint torques (Fig. 2, B and D, switch \( a \) is in position 1, switch \( b \) is in position 2). The Dyn2 controller, in contrast, used the predicted arm-state signal (calculated the same way as in Kin2) as the input signal to the IDM (Fig. 2B, both switches \( a \) and \( b \) are in position 2). The IDM in Fig. 2B could be the same putative internal inverse-dynamics model that generated the feedforward torque output signal or a separate IDM that is a component of the online correction mechanism.

The gain (G; Fig. 2B) of the correction signal was systematically varied to find the best fits of model arm movements to human trajectories. The range for Kin1 and Kin2 controllers was 0.05–0.5, in 0.05 increments; the range for Dyn1 and Dyn2 controllers was 0.005–0.05, in 0.005 increments. The difference between the gain values of the kinematic and dynamic controllers is because of the differences in units of position and torque used for correction in the Kin and Dyn controllers, respectively.

Model and human trajectories were compared across controllers with different gains and all other parameters (feedback delays and viscosity) being equal to determine the best performance for each controller. Three measures were used to evaluate the similarity between the simulated and human trajectories: velocity error, onset error, and endpoint error. These measures were relatively independent with correlation coefficients between them being <0.5. The velocity error was calculated by summing across time the perpendicular distances between model and human endpoint velocity values for each T2 location. The onset error was calculated as the difference between the onsets of online correction in human and simulated trajectories. The onset of correction in the model trajectories were calculated by measuring the human tangential angles at the onsets of online correction described above (see Analysis) and finding the times at which the model tangential angles reached the same values. The endpoint error was the difference between the human and simulated endpoint errors. The human endpoint errors were calculated as distances between the target positions and the corresponding human trajectories at the end of movement. The endpoint errors of the simulated trajectories were calculated the same way at times equal to the mean durations of human control and target-jump trajectories. The best performance of the four controllers was defined as the smallest sum of the squared normalized error measures described above. The errors were normalized to their means for equal contribution to the sum. Combinations of other measures and different combinations of the same three measures were also tested for comparing performance of the four models to human performance. All measure combinations selected the same two controllers to be the best and the worst performers, but the distinction between the other two controllers depended more on the particular choice of measures.

RESULTS

Human behavioral performance

Visually guided movements were studied in a double-step paradigm, which required subjects (\( n = 8 \)) to both look and point to visual targets projected in the plane of their movement (Fig. 1A). Subjects responded to the appearance of a visual target, T1, in one of two locations (T1\(^{30} \) or T1\(^{30} \)) 15 cm away from the start location. Subjects first initiated an ocular saccade at 204 ± 40 (SD) ms latency and later moved their hand toward the T1 target 264 ± 35 ms after its appearance (Fig. 1C; Supplementary Table S1).\(^1\) The arm movement was carried out at the subject’s preferred speed, and the peak velocity was on average 0.75 ± 0.2 m/s across subjects. Characteristic examples of hand trajectories are shown from a subject with mean peak velocities of 0.63 ± 0.09 and 0.70 ± 0.09 m/s averaged across trials to T1\(^{60} \) and T1\(^{30} \), respectively (Fig. 3A) and from a different subject with mean peak velocities of 0.94 ± 0.26 and 1.07 ± 0.27 m/s averaged across baseline trials to T1\(^{60} \) and T1\(^{30} \), respectively (Fig. 3B).

In one half of the trials, T1 did not change position (baseline trials). In the other half, the target jumped to one of eight other locations centered on T1 (T2\(^{3.5} \), T2\(^{7} \), T2\(^{10.5} \), T2\(^{14} \); Fig. 3). This corresponded to target displacements ranging from 1 to 4° visual angle. The jump was triggered by the onset of the subject’s ocular saccade and occurred on average 50 ms before the start of arm movement, during the period of saccadic suppression of vision (Bridgeman et al. 1975; Mackay 1970; Matin 1974). The target jump triggered a corrective saccade directed toward the new target location, which occurred on average 233 ± 76 ms after the target jump or 208 ± 77 ms after the termination of the first saccade (Supplementary Table S1). Furthermore, all subjects responded to the target jumps by initially following their baseline reach trajectory toward the T1 target and later deviating the trajectory toward the T2 target (Fig. 3). Most subjects corrected their trajectories gradually with one smoothly curved movement whose deviation from the baseline began about half way to T1 and scaled with the size of the target jump from its onset (Fig. 3C). However, the two fastest-moving subjects showed relatively small trajectory deviations until their hand was close to T1 and made a sharp change in movement direction (Fig. 3D). This was not caused by delayed corrective responses or inattention to the target jumps because the time of onset of the trajectory deviations was similar in all subjects (Fig. 3, C and D). This suggests that the fast-moving subjects had nearly reached T1 before the on-line correction mechanism could influence the reaching trajectories, possibly compounded by the lower effectiveness of the error feedback pathway in overcoming the higher momentum of the fast-moving arm. This interpretation is explored further with modeling.

Consistent with earlier studies (Blouin et al. 1995; Bridge- man et al. 1975; Niemeier et al. 2003), the amplitude of the target jumps determined whether the subjects were aware of the perturbation. Subjects’ reports at the end of each trial showed that small target jumps went unperceived in most trials caused by saccadic suppression, whereas most large target jumps were noticed and reported by the subjects (Fig. 4A). Subjects also reported a false positive rate of 6% perceived jumps in baseline trials when none had occurred (Fig. 4A). The mean trajectory path for trials with unreported target displacements tended to be displaced further away from the unperturbed trajectory to T1 and appeared to be slightly less curved than trials in which the displacement was detected and reported by the subjects (Supplementary Fig. S1A). However, for the smaller target displacements the mean paths for the unreported-displacement trials were within the confidence intervals of the

\(^1\) The online version of this article contains supplemental data.
Trajectories in the reported-displacement trials (Supplementary Fig. S1B). In contrast, for the largest two displacements, the mean paths of the few unreported-displacement trials clearly lay outside of the CI of the majority of reported-displacement trials for part of their path, and there was even some indication that the trajectories lay outside of the usual range of trajectories directed at T1 from the onset of the reaching movements (Supplementary Fig. S1A).

On average, the trajectory corrections started at the same time regardless of the amplitude of the target jump and the accompanying changes in overall degree of perceptual awareness of the displacements (Figs. 3, C and D, and 4B). Note that the onset of trajectory corrections was calculated relative to the onset of hand movement, whereas the target jump was triggered on average 50 ms before the onset of hand movement (Fig. 1C). Statistical analysis of mean trajectory-correction onset times using repeated-measures ANOVA with main factors initial target position (T1 factor with 2 levels) and signed target jump amplitude (T2 factor with 8 levels) found no significant differences between the onset values (T1 factor: \( F = 0.22, P = 0.65 \); T2 factor: \( F = 2.31, P = 0.12 \); interaction between factors: \( F = 0.29, P = 0.77 \)). Therefore these results suggest that early trajectory corrections begin at about the same time regardless of both the size of the jump (at least down to 3.5° reach direction changes) and the level of conscious awareness of the target jump by the subjects. Trial-by-trial analysis yielded essentially the same results (data not shown).

Both angular and perpendicular linear deviations between the jump-trial trajectories and the baseline trajectories, averaged across both movement and target jump directions and across subjects, gradually increased with the amplitude of the target jump (Fig. 5, A and B). When the angular and perpendicular deviations for each target-jump amplitude were normalized to their maximal deviations at 0.48 s after the start of movement, all traces closely overlapped (Supplementary Fig. S2). This further supports our conclusion that trajectory corrections for all target jumps started at the same time and scaled linearly with the amplitude of the target direction displacement throughout the duration of the corrective response. The amount of scaling of trajectory deviations was estimated by fitting a linear regression between the amplitude of the target jump and the tangential angles of jump-trial trajectories at different times during movement. The angle of the fitted linear regression line increased gradually following the target jump so that by the time the hand reached peak velocity the trajectory corrections were already scaled proportionally to the amplitude of the target jump (Fig. 5C). The regressions shown in Fig. 5C were highly statistically significant for trajectory deviations at and following peak velocity \( (R^2 = 0.984 \) and 0.964 for trajectory angles at 165 ms for T160 and T130, respectively, \( R^2 = 0.998 \) and 0.996 for trajectory angles at 290 ms for T160 and T130, respectively, \( P < 0.01 \) in all cases). However, no significant trajectory deviations were observed before peak velocity and consequently regressions were insignificant \( (R^2 = 0.176 \) and
linear fit would indicate a saturation of error correction at large $A$; linear fits explained a large percentage of the variance in $G$). However, trajectory corrections with the target jumps (Fig. 1) showed no obvious pattern and were of similar amplitude across all subjects and T1 targets.

To further test the linearity of error correction we compared the quality of linear, quadratic, and sigmoidal fits to the scaling of individual-subject trajectories at and following peak velocity (Fig. 6, A and B). Better sigmoidal fit than a linear fit would indicate a saturation of error correction at large target jumps in the two opposite directions (Fig. 1F), whereas better quadratic fit would indicate a nonlinear scaling of trajectory corrections with the target jumps (Fig. 1G). However, linear fits explained a large percentage of the variance in trajectory deviations at peak velocity in six of eight subjects (Fig. 6A; $R^2$ for subjects 1–8 = 0.72, 0.57, 0.95, 0.97, 0.91, 0.99, 0.98, and 0.01, respectively); the same was true in all subjects for trajectory deviations 125 ms after peak velocity (Fig. 6B; $R^2$ for subjects 1–8 = 0.99, 0.95, 0.98, 0.98, 0.996, 0.99, 0.998, and 0.88, respectively). Fitting a sigmoidal function increased the amount of explained variance by 5% compared with linear fits for trajectory deviations at peak velocity. However, this increase was driven by only two of eight subjects, whose trajectory deviations were fitted better with sigmoidal compared with linear fits (12 and 9% increases in explained variance for subjects 2 and 5, respectively). However, this difference all but disappeared 125 ms later, where sigmoidal fits of trajectory deviations increased the explained variance by only 1% over the linear fits. Fitting a quadratic function decreased the amount of explained variance compared with linear fits by $-43$ and $-23\%$ for trajectory deviations at and following peak velocity, respectively. The comparison of sigmoidal, quadratic, and linear fits of the mean trajectory deviations shown in Fig. 5C yielded similar results (linear fit $R^2 = 0.968, 0.960, 0.998, 0.995$, quadratic fit; $R^2 = 0.655, 0.478, 0.886, 0.852$; sigmoidal fit $R^2 = 0.985, 0.999, 0.999, 0.996$ for T1$^{160}$ at 165 ms, T1$^{30}$ at 165 ms, T1$^{60}$ at 290 ms, and T1$^{30}$ at 290 ms, respectively). This amounts to the mean difference in explained variance between the linear and sigmoidal fits of 3 and 0.1% for trajectory deviations at and following peak velocity. The mean difference in explained variance between the linear and quadratic fits is $-41$ and $-13\%$ for trajectory deviations at and following peak velocity. Thus this analysis indicates that most subjects showed essentially linear scaling of trajectory adjustments with the amplitude of the target jump. Regression on a sigmoidal function, consistent with saturation of error corrections for large target displacements, did not account for a significantly greater amount of the variance of the performance overall for most subjects at any time during the reaching movements.

When linear regressions were fitted to trajectory deviations in 10-ms steps from the onset of hand movement (Fig. 6C), the angle of the regression line was statistically significantly different from zero starting at 123 ± 24 ms (averaged across subjects) after the start of movement. The data from individual subjects also show that the temporal evolution of trajectory corrections was scaled to the duration or peak velocity of each subject’s movement, so that corrections were always completed just as the hand arrived at the target (Fig. 6E).

These results show that the trajectory correction was proportional to the amplitude of the target jump from its onset, linear across the entire tested range of target jump amplitudes, and scaled to the speed of movement of each subject. Furthermore, there was no evidence of an early correction phase that saturated for large target jumps, followed by a later correction that scaled for the entire range of tested target displacements, which would be consistent with a two-stage online correction process. This suggests that a single corrective mechanism that is proportional to error amplitude may underlie online correction for target jumps in this study. Furthermore, the observed linear relationship between the amplitude of the target jump and trajectory correction suggests a constant gain of error feedback in the corrective mechanism.

Modeling studies

Assuming a one-stage proportional correction mechanism as suggested by the human performance in the target-displacement study, we next assessed the ability of four simple control circuits with different types of error feedback and motor command corrective signals to replicate the kinematics of the online corrections. Two general types of error correction path-

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FIG. 4. A: effectiveness of the saccadic suppression for target jumps of different amplitude. Jump angle values are in a hand-centered coordinate system. Incidence of reported jump values are mean percentages of reported target jumps ± SD, averaged across all subjects and T1 targets. B: onsets of online correction relative to the start of hand motion. Plotted values are means ± SD across all subjects and T1 targets.

0.256, $P = 0.65$ and 0.51 for trajectory angles at 64 ms for T1$^{160}$ and T1$^{30}$, respectively). Residuals of these linear fits showed no obvious pattern and were of similar amplitude across the regression slopes (Fig. 5D), which indicates that linear regression is an appropriate fit for the trajectory-deviation data. To further test the linearity of error correction we compared the quality of linear, quadratic, and sigmoidal fits to the scaling of individual-subject trajectories at and following peak velocity (Fig. 6, A and B). Better sigmoidal fit than a linear fit would indicate a saturation of error correction at large target jumps in the two opposite directions (Fig. 1F), whereas better quadratic fit would indicate a nonlinear scaling of trajectory corrections with the target jumps (Fig. 1G). However, linear fits explained a large percentage of the variance in trajectory deviations at peak velocity in six of eight subjects (Fig. 6A; $R^2$ for subjects 1–8 = 0.72, 0.57, 0.95, 0.97, 0.91, 0.99, 0.98, and 0.01, respectively); the same was true in all subjects for trajectory deviations 125 ms after peak velocity (Fig. 6B; $R^2$ for subjects 1–8 = 0.99, 0.95, 0.98, 0.98, 0.996, 0.99, 0.998, and 0.88, respectively). Fitting a sigmoidal function increased the amount of explained variance by 5% compared with linear fits for trajectory deviations at peak velocity. However, this increase was driven by only two of eight subjects, whose trajectory deviations were fitted better with sigmoidal compared with linear fits (12 and 9% increases in explained variance for subjects 2 and 5, respectively). However, this difference all but disappeared 125 ms later, where sigmoidal fits of trajectory deviations increased the explained variance by only 1% over the linear fits. Fitting a quadratic function decreased the amount of explained variance compared with linear fits by $-43$ and $-23\%$ for trajectory deviations at and following peak velocity, respectively. The comparison of sigmoidal, quadratic, and linear fits of the mean trajectory deviations shown in Fig. 5C yielded similar results (linear fit $R^2 = 0.968, 0.960, 0.998, 0.995$, quadratic fit; $R^2 = 0.655, 0.478, 0.886, 0.852$; sigmoidal fit $R^2 = 0.985, 0.999, 0.999, 0.996$ for T1$^{160}$ at 165 ms, T1$^{30}$ at 165 ms, T1$^{60}$ at 290 ms, and T1$^{30}$ at 290 ms, respectively). This amounts to the mean difference in explained variance between the linear and sigmoidal fits of 3 and 0.1% for trajectory deviations at and following peak velocity. The mean difference in explained variance between the linear and quadratic fits is $-41$ and $-13\%$ for trajectory deviations at and following peak velocity. Thus this analysis indicates that most subjects showed essentially linear scaling of trajectory adjustments with the amplitude of the target jump. Regression on a sigmoidal function, consistent with saturation of error corrections for large target displacements, did not account for a significantly greater amount of the variance of the performance overall for most subjects at any time during the reaching movements.

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Modeling studies

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ways were tested: kinematic correction (controllers Kin1 and Kin2) and dynamic correction (controllers Dyn1 and Dyn2) (Fig. 2). Controller Kin1 relied on the kinematic error between the desired and sensed direction of reach movement toward the target. Controller Kin2 calculated the error signal the same way as Kin1, but instead of the delayed peripheral feedback-mediated estimate of arm state, the FDM was used to predict reach direction based on an efference copy of the outgoing motor command. The other type of error correction circuit simulated here included an IDM, which transformed the kinematic directional error into the corrective joint torques appropriate for the dynamics of the virtual arm. The internal IDM of the Dyn controllers could be the same putative IDM that calculated \( T^1 \) or could be a separate internal model that is integral to the online correction mechanism. The kinematic error before its transformation by the IDM in the Dyn1 and Dyn2 controllers was calculated the same way as in the Kin1 and Kin2 controllers, respectively.

The best performance of the four controllers is shown in Figs. 7–9. The feedback delays were the same across controllers, but the gains of the error signal were chosen so that the models generated trajectories that were the closest to those of human subjects for movements toward the T160 target (Fig. 7). All controllers drove the virtual arm with gradually deviating trajectories that scaled with the target jump amplitude (Fig. 8). However, there were large differences in the success of trajectory corrections for the target jumps by different types of controllers (Supplementary Table S2).

The Kin1 controller with a delayed kinematic error signal can accomplish trajectory corrections during very slow movements (Supplementary Fig. S3). However, during movements at the speeds performed by the subjects, the Kin1 controller produced asymmetric trajectory deviations that were hypometric for clockwise target jumps and hypermetric for counterclockwise target jumps (Fig. 7B). Choosing a smaller or a larger gain of error signal decreased or increased, respectively, the amount of deviation at any given time between the jumptrial trajectories, but did not appreciably change the undershoot/overshoot pattern of corrections. Furthermore, the overall fit between the model and human trajectories was poor (Figs. 8A and 9, A and B; Supplementary Table S2). This shows that a simple delayed kinematic error correction mechanism is insufficient for online correction for target jumps and produces trajectories that are very dissimilar to trajectories observed in humans.

The failure of the Kin1 controller was clearly movement speed dependent, which may indicate that the delay of the arm state estimation based only on peripheral afferent feedback caused the error signal to be too delayed to correctly adjust the ongoing movement at the movement speeds performed by the subjects. Compensation for the delay by the FDM in the Kin2 controller slightly improved the performance of the simulation (Figs. 7C and 8B; Supplementary Table S2). However, the Kin2 controller still produced asymmetric trajectory corrections with inappropriate velocities (Fig. 9C) so that the endpoint trajectory did not come close to the targets at the mean movement time of human subjects. Note, that the illustrated trajectories only show the first 500 ms of model performance. When the model was allowed to run longer, it could eventually bring the endpoint to the target after a few terminal oscillations (Supplementary Fig. S4), provided that the gain of the error-correction pathway was not too high to cause instability.

In contrast, the Dyn1 and Dyn2 controllers produced much more symmetric trajectory corrections (Figs. 7, D and E, 8, C and D). The Dyn1 controller largely eliminated the target overshoots and undershoots evident in the Kin1 and Kin2

![Figure 5](http://jn.physiology.org/)

**FIG. 5.** A: time evolution of absolute angular deviations of target-jump trajectories relative to baseline trajectories. Means were calculated across all T1 targets, directions of target jumps, and subjects. Shaded areas indicate SE across subjects. B: time evolution of absolute linear deviations between target-jump and baseline trajectories. Means were calculated across all T1 targets, directions of target jumps, and subjects without normalization. Shaded areas indicate SE across subjects. C: angular deviations of hand trajectories at different times during the movement. Circles are means, error bars indicate SD across subjects, and thick lines are regression fits to the data. Angles were calculated at the moment the subjects reached 50% of the peak velocity during the acceleration phase (green lines), at peak velocity (black lines), and at 50% of peak velocity during the deceleration phase (red lines). The inset shows these times relative to a stylized velocity profile; they are also shown in A. Dashed lines, T110 direction; solid lines, T160 direction. D: residuals for the regressions in C; color coding is the same as in C. Residuals of regressions fitted to angular deviations in C show no common pattern of dependence on jump amplitude, which indicates a good fit of linear regressions.
the internal forward model-based predicted arm state estimate to calculate the kinematic error and passed the error signal through an IDM to calculate the additive joint torque signal necessary to implement the correction while simultaneously compensating for limb dynamics.

The Dyn2 controller can also simulate the differences in performance of the individual subjects illustrated in Fig. 3. We used the same model parameters that produced the best fit to the mean trajectories (Fig. 7E), but scaled the feedforward torque command to produce movements to the T1 target with the same peak velocities as that of the two subjects in Fig. 3 (Fig. 10). The peak velocities of baseline movements to the T1 target in subjects shown in Fig. 3, A and B, were 0.63 ± 0.09 and 0.94 ± 0.26 m/s, respectively, whereas the peak velocities of the model arm produced by the Dyn2 controller with scaled \( \tau^{T1} \) in Fig. 10, A and B, were 0.62 and 0.95 m/s, respectively. Both trajectory shapes and temporal evolution of subject’s movements were reasonably well matched by the model with the same values of gain, viscosity, and delays, but with different velocity of the feedforward motor command. This simulation indicates that the differences in the trajectories of the two subjects in Fig. 3, C and D, were explained primarily by the kinematics and dynamics of the more rapid movements of the subject in Fig. 3D and not because of differences in the timing or gain of the rapid on-line correction mechanism.

In summary, modeling results of this study show that a motor controller that sums a feedforward motor command with an error correction signal is capable of rapidly correcting for unexpected target displacements. The best performance was obtained with a controller circuit that used a forward model to compensate for afferent delays in arm state estimation and an inverse-dynamics model to account for limb dynamics to calculate the error correction signal. This controller produced responses of a simple arm model that closely approximated the performance of human subjects as they correct ongoing movements for target displacements.

**DISCUSSION**

This study yielded two main findings. First, we found no evidence of a hypothesized change in the scaling of the short-latency corrections for small versus large target displacements that would be consistent with a two-stage mechanism of online correction. Thus we found no evidence in the moment-to-moment kinematics of the reach trajectories of a credit-assignment process that influenced how the motor system responded to random target displacements of different sizes. However, this does not preclude the possibility of a credit-assignment process that influences how the motor system responds to and gradually adapts to repeated target displacements of different sizes (Berniker and Kording 2008; Ingram et al. 2000; Kagerer et al. 1997; Kluzik et al. 2008; Malfait and Ostry 2004; Wie and Kording 2009). Second, we found that the kinematics of online corrections of human subjects, at least for the tested range of target jumps, could only be approximated reasonably well by a single error correction mechanism that uses an internal forward model to compensate for peripheral feedback delays and uses an inverse model of the limb to adjust the outgoing predictive motor command to the original target location in a way that takes into account the dynamical properties of the limb. A number of modeling studies have suggested that the motor circuits that control unperturbed reaching movements and that compensate for external force-field perturba-
tions require combinations of forward and inverse internal models to generate the appropriate predictive feed forward motor output commands (Bhushan and Shadmehr 1999; Haruno et al. 2001; Wolpert and Kawato 1998). Our modeling study indicates that the same control architecture is also necessary to reproduce the feedback-mediated trajectory adjustments observed as human subjects correct for trajectory errors resulting from unexpected target displacements. Without the forward and inverse internal models, feedback delays and the inherent dynamics of the limb would result in reach trajectories that cannot compensate rapidly for even small shifts in target location.

One-stage versus two-stage online correction

Our results showed that the early online correction is triggered at the same onset time by all target jump amplitudes and directions (Figs. 4–6; Supplementary Fig. S2). The onset latency values are consistent with previous findings for the timing of responses to visual perturbations (Day and Lyon 2000; Prablanc and Martin 1992; Sarlegna et al. 2003). Furthermore, our results have shown that the amount of trajectory correction at all times during the movement is linearly proportional to the amplitude of the target jump across the entire range of tested target displacements (Fig. 3C; Supplementary Fig. S2). If the size of the correction of reach trajectory mediated by the rapid online mechanism does saturate at some maximum value, it must only occur for target displacements that are larger than those used in this study. Finally, the performance of the human subjects did not show evidence of an abrupt transition in the kinematics of the rapid corrective responses for small versus large target displacements. There was therefore no evidence in this study of a process that might have attributed performance errors to different causes such as motor execution variability versus changes in the environment and corrected for them with different mechanisms. This suggests that a single error correction mechanism may be responsible for the observed online correction. However, it is important to point out that the absence of observable nonlinearities in the kinematics of corrections for target displacements of different amplitudes does not preclude the possibility of two corrective mechanisms with overlapping or staggered delays and variable gains. This
complex situation cannot be discounted using the current paradigm. Moreover, it is possible that the inherent dynamical properties of the arm may have filtered out any physical evidence of a two-stage correction mechanism for larger target displacements, especially if the latency difference between the two processes was not too large.

Consistent with published observations, we found that subjects were largely unaware of small target jumps but became progressively more aware of target jumps as their amplitude increased (Blouin et al. 1995; Niemeier et al. 2003). Nevertheless, subjects succeeded in reaching the final target positions whether or not they were aware of the displacement. This supports previous studies showing that awareness of the visuomotor errors does not have a causal relationship with the online correction of hand trajectories (Castiello et al. 1991; Fecteau et al. 2001; Johnson et al. 2002). However, there was some suggestion of a relationship between reach trajectory shape and the likelihood of being aware of the target displacement. Especially for the largest target displacements, the reach trajectory during the relatively infrequent trials in which the subjects failed to report the displacement tended to be directed away from the original target location and toward the displaced position almost from the beginning of the movement and showed less curvature of the corrected trajectory compared with those trials in which the subjects reported the displacement. It is unlikely that these trajectories that deviated away from T1 from their outset were produced by a very precocious rapid correction response. Instead, they may simply be trials whose initial direction was at the extreme of the natural distribution of variability of initial reach directions toward T1. Although very speculative at this point, it is possible that when subjects make a reaching movement to T1 with an initial directional error that is larger than normal and by chance is in the same direction as the ensuing target jump, they may be less likely to detect a large target displacement in the same direction.

Previous studies of the rapid online error correction mechanism for target displacements during reaching movements focused primarily on such issues as its short latency, independence from perceptual processes, insensitivity to cognitive
control, and the possible implication of dorsal stream visuomotor pathways (Day and Lyon 2000; Goodale et al. 1986; Pelisson et al. 1986; Prablanc and Martin 1992; Rossetti et al. 1995; Sarlegna et al. 2003). This study provides the most detailed description to date of the kinematics of the early corrective response and its relation to the size of target directional changes.

**Online correction by summation of feedforward and feedback error signals**

To investigate the mechanism of the simplest necessary error-correction signal for successful online corrections for target displacements we tested the performance of 4 versions of a controller with features inspired by experimental observations in moving a dynamic model of the arm with physiological parameters. The simplest model of the observed linear relationship between the error and trajectory correction in humans is one that multiplies the error with a constant scaling factor (gain) and incorporates the result into the ongoing motor command. Similarly, the simplest model of the observed common onset of trajectory corrections for target jumps of different amplitudes is one with a single corrective pathway and a constant feedback delay. Our modeling results show that a controller with such attributes can produce motions of a simple dynamic model of a 2-joint arm that closely approximate key features of human reach trajectories. This suggests that a single proportional error-correction mechanism can compensate for visuomotor errors of different amplitudes and that this mechanism is of sufficient gain to adjust for even the largest errors tested in this study.

Further support for this hypothesis is that the rate at which the trajectories deviate away from the baseline also scaled as a function of the overall movement velocity for each subject (Fig. 3D). This provides indirect evidence that the error signal is continually proportional to the difference between the target location and current estimate of hand position but also suggests that the rate at which the error is corrected is proportional to the overall speed and movement duration of each subject. This indicates a close coordination between the time course of the online correction mechanism and the time course of the ongoing movement. This coordination could be achieved by efferent feedback signals about the speed of movement, an efference copy-based estimate of the time course of changes in arm state, or both.

**FIG. 9.** Evolution of velocity vector amplitude in time. Solid lines, counterclockwise (CCW) target jumps; dashed lines, clockwise (CW) target jumps. Black lines are velocities of control trajectories. A: velocity of human subjects, same trajectories as in Fig. 7A. B–E: velocity of model, same trajectories as in Fig. 7, B–E. Asymmetricity of corrections produced by Kin controllers is shown by unequal velocities for CW and CCW target jumps in B and C, which is absent in human data in A and in velocities of movements produced by Dyn controllers in D and E.
The complexity of the error signal independently from the feedforward signal and had the two signals summate to drive a two-joint arm model. We found that the controller that summed dynamic feedforward and corrective signals could reproduce the recorded human movements reasonably closely, suggesting that it is a viable control strategy for fast online motor control. This is consistent with multiple modeling studies suggesting that movement planning and execution includes multiple overlapping pathways that accomplish optimal multisensory integration based on both afferent feedback and internal predictive signals (Bhushan and Shadmehr 1999; Flanagan et al. 1993; Mehta and Schaal 2002; Nijhof 2003; Sabes 2000; Shadmehr and Krakauer 2008; Wolpert and Kawato 1998). Although most of these studies include both dynamic and kinematic signals in their models of motor control, this is the first study to address the need for dynamics and delay compensation in the error correction pathway separately from the feedforward motor command.

The results of our study strikingly show that controllers with only kinematic error correction (Kin1 and Kin2) were unsuccessful in compensating for target jumps: even though the largest target displacements were only 14°, the feedforward motor command included all the necessary compensation for limb dynamics for movements to the original target, and the model incorporated joint viscosity that simulated resistance to imposed movement by soft tissues of the limb and provided intrinsic partial dynamics compensation. This failure to reproduce human trajectories by Kin controllers is not because of the inherent inability of kinematic correction to compensate for motor errors (Supplementary Fig. S3). When the models simulated slow movements to minimize interaction torques (Supplementary Fig. S3) or were allowed to run beyond the average human movement time (Supplementary Fig. S4), the kinematic correction signal by itself was sufficient to eventually bring the model arm endpoint to the target position after multiple oscillations around the target, provided that the gain of the error signal was not too large to make the model behavior unstable. However, both controllers with delayed and delay-compensated kinematic error correction caused large and asymmetric trajectory deviations and did not bring the model arm close to the targets within a realistic time frame. These large asymmetric deviations produced by Kin controllers arose because the corrective movements evoked by the purely kinematic error signals produced additional interaction torques that were not accounted for in the original motor command to T1 or in the kinematic correction signal itself. This result suggests that the error signal of the online correction mechanism has to account for the complex dynamics of whole arm movements, such as the interaction torques that arise during movement of a multi-segment limb (Hollerbach and Flash 1982). This conclusion is consistent with a recent study showing that adaptation to novel dynamics modifies not only movement planning but also the online control of movement (Wagner and Smith 2008). Together the results of Wagner and Smith (2008) and our modeling results suggest that both movement planning and online control rely on a common internal model of limb dynamics.

Based on the observations that the onset of online correction can be shorter than the usual “voluntary” motor responses to sensory stimuli, it was suggested that the nervous system may rely on predictive internal estimates of current arm state to compute corrections for target jumps (Cooke and Diggles...
In our study, both kinematic and dynamic controllers that relied only on delayed arm state estimation performed worse than the corresponding controllers with delay-compensated internal estimation of arm state. This improvement occurred despite setting the delayed feedback controllers according to the “best case scenario” by including the shortest feedback delays reported in the literature and using the feedforward motor command that produced movements of average speed. Therefore our simulations suggest that the predictive estimation of arm state is an important part of the error computation for online correction for target displacements, especially if the motor system relies on superimposed feedforward and corrective pathways. This is in agreement with multiple studies arguing the importance of efference copy signals for online control of movement (Desmurget and Grafton 2000; Kording and Wolpert 2006; Sabes 2000).

Model limitations

Mathematical models of how the hybrid feedforward/feedback motor command can be generated by the motor system and how it interacts with the musculoskeletal system tend to be complex, and, therefore can simulate various aspects of human behavior (Bhushan and Shadmehr 1999; Flanagan et al. 1993; Shadmehr and Krakauer 2008; Wolpert and Kawato 1998). Higher model complexity can increase its predictive power, but it inevitably requires many ad hoc assumptions because of the lack of experimental data measuring all the necessary parameters, which can limit the physiological relevance of the model. In our study, we used a simple dynamic model of a two-joint arm driven by a controller with either kinematic or dynamic error correction signals. All four parameters that defined the behavior of the model were varied to find the simplest working controller. However, this simplicity also created a few limitations. The main limitation is the lack of musculature with all the complexity of muscle anatomy and physiology. This complexity of the muscular system may simplify neural control signals, for example, by providing some inherent dynamics compensation (Feldman 1986; Flanagan et al. 1993; Gribble et al. 1998). The second limitation is that the controllers tested in this study all combined feedforward and corrective signals with constant gains throughout the movement. However, it is sometimes proposed that a shift from preplanned to online control occurs during movement by changing the gain of feedback (sensory) pathways (Wolpert et al. 1995). Third, the controllers tested here do not take into account any long-loop (voluntary) error-correction pathways that may contribute to online control, for example those that would change the feedforward motor command to be more appropriate for the newly displaced target location. Instead, the controllers used a feedforward motor command aimed at the original target location for the duration of the response. The absence of voluntary corrections and changing feedback gains may explain larger final errors shown by the model compared with those shown by the subjects. These more complex pathways may also be more critical for recalculating the outgoing motor command to correct for larger target jumps than those used here, such as reversals of target locations (Georgopoulos et al. 1983). Last, the horizontal planar configuration of the model only partially captures the kinematics of the full three-dimensional configuration of the arm associated with the observed two-dimensional hand trajectories in humans. This difference between model and human arm configurations may also account for some of the observed differences between the human and the best simulated model trajectories in this study. However, that should not explain the relative ability of the different controllers to produce effective corrective responses of the simple arm model to the target displacements. Nevertheless, a more quantitative comparison between human and model performance would undoubtedly require a three-dimensional model of the arm and full three-dimensional kinematics of human movement.

Conclusions

Our study has shown that goal-directed reaching movements can be supervised by a single fast online correction controller that robustly compensates for visuomotor perturbations of different amplitudes and directions. Furthermore, this study found that online control of reaching movements can be accomplished by superimposing a dynamically appropriate error correction gated by a constant gain onto the outgoing feedforward motor command to the original target. This organization of the human online correction mechanism may be exploited to develop new strategies for assessment and rehabilitation of motor deficits following brain damage. For example, it may be possible to dissociate between damage to the feedforward and corrective components of the proposed controller and customize the rehabilitative intervention to target the identified pathway. Furthermore, the proposed importance of dynamics compensation for the online control of goal-directed movements suggests that focusing rehabilitation on movement dynamics, i.e., retraining appropriate muscle activity patterns, may be more beneficial than focusing on recreating normal movement kinematics alone.

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