

# **RESEARCH ARTICLE**

Control of Movement

# Inverting a model of neuromuscular control to estimate descending activation patterns that generate fast-reaching movements

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# Abstract

Reaching movements generally show smooth kinematic profiles that are invariant across varying movement speeds even as interaction torques and muscle properties vary nonlinearly with speed. How the brain brings about these invariant profiles is an open question. We developed an analytical inverse dynamics method to estimate descending activation patterns directly from observed joint angle trajectories based on a simple model of the stretch reflex, and of muscle and biomechanical dynamics. We estimated descending activation patterns for experimental data from eight different planar two-joint movements performed at two movement times (fast: 400 ms; slow: 800 ms). The temporal structure of descending activation differed qualitatively across speeds, consistent with the idea that the nervous system uses an internal model to generate anticipatory torques during fast movement. This temporal structure also depended on the cocontraction level of antagonistic muscle groups. Comparing estimated muscle activation and descending activation revealed the contribution of the stretch reflex to movement generation that was found to set in after about 20% of movement time.

**NEW & NOTEWORTHY** By estimating descending activation patterns directly from observed movement kinematics based on a model of the dynamics of the stretch reflex, of muscle force generation, and of the biomechanics of the limb, we observed how brain signals must be temporally structured to enable fast movement.

inverse model; motor control; reaching movements; reflex system

# INTRODUCTION

Humans move their hands toward objects on gently curved paths that have a temporal profile that is smooth and largely invariant across workspace and movement speeds (1, 2). To achieve such invariant kinematics, muscles must be activated at the right time and to the right extent in ways that vary across workspace. The forces generated by muscles evolve in time in a way that depends on the rate of change of muscle activation and muscle length. The active torques generated by muscle forces at each joint perturb other joints through interaction torques that through inertial, centrifugal, and Coriolis coupling vary nonlinearly with joint velocity (3). What kind of neural activation patterns does the brain need to generate to bring about the invariant and smooth kinematic profiles given the variant and rate-dependent muscular and mechanical constraints? This is a central question in the field of motor control often framed as the problem of the "internal model," that is, the problem of how

the brain "computes" the required neural signals that will bring about the right set of muscle forces that take into account all these complexities of the muscle-joint system (4). The methods of computational motor control have been used to characterize the performance of the nervous system with respect to such questions (5) and extensive empirical work has been aimed at understanding the adaptive mechanisms through which such internal models may adapt to changing properties of the plant or of its mechanical environment (6).

The argument has been made that spinal reflex circuitry may simplify this control problem (7), in effect relieving the brain to some extent of the task of computing specific neural signals that compensate for the muscle properties and mechanical coupling. In the limited case of perfect peripheral control, the brain would need to plan movement only at a kinematic level in very simple and invariant ways and leave all the detailed control to spinal reflexes (8). In recent work from our group, we explored this issue by using the



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0022-3077/24 Copyright © 2024 The Authors. Licensed under Creative Commons Attribution CC-BY 4.0. Downloaded from journals.physiology.org/journal/jn (A202:0900:0A67:800:B590:5411:4D92:A302) on September 4, 2024. bimechanical dynamics, a model of the dynamics of muscle force generation, and a simple model of the stretch reflex to estimate the minimal change in descending activation that is needed to bring about smooth movements of the hand to a target location (9). We found that such minimally changing descending activation patterns are not invariant across the workspace and do not scale in a simple way when the speed of movement is varied. This refuted the hypothesis that the stretch reflex and muscle properties alone render superfluous the temporal structuring of descending activation patterns postulated in the internal model framework. Only in the limited case of slow movements was the minimally changing descending activation pattern ramp-like consistent with the equilibrium point hypothesis (10).

The nervous system does not necessarily use a "minimally changing" descending activation pattern to generate movement. In fact, in this earlier work, we found discrepancies between the predicted and observed kinematics that stem from the fact that more change in descending activation is needed to accelerate than to slow down joint motion (a fact that comes from the larger forces generated by muscles when they lengthen than when they shorten). If we were able to directly estimate the descending activation pattern needed to generate any particular movement, we could directly observe how the brain solves the internal model problem. We could also determine the extent to which reflexes support or hinder movement.

In this paper, we make a first attempt at such a direct estimation. We use the same set of models of mechanical, muscle, and reflex dynamics as earlier, but now analytically invert that model. This enables us to directly determine from experimentally observed movement trajectories the descending activation patterns that the modeled system would need as input to generate the observed movements. This inversion requires further simplifications, whose validity we assess in part by testing if the forward simulations of the model are consistent with the initial data. We perform this analysis for a set of experimental trajectories obtained at two different overall movement speeds and observe how descending activation is reshaped with movement speed. We also assess when and how strongly the stretch reflex contributes to the joint torques that accelerate and decelerate joint motion.

# **METHODS**

#### **Estimation Method**

The estimation approach was developed around an experimental data set that probed the targeted movement of the hand at two overall movement speeds. Movement of the arm was limited to the shoulder and elbow joint operating within a horizontal plane (Fig. 1). Planar movement was obtained by instruction, avoiding the isometric forces that may arise when pushing against a manipulandum (11). The table height was adjusted to the height of the shoulder of the sitting participant. Additionally, participants were strapped to the chair with a belt near their right shoulder to limit trunk movement. To limit wrist movement, the wrist was strapped into a splint.



**Figure 1.** Top view of the experimental set-up with sampled movements. The participant is seated in front of a horizontal monitor with the center of his or her shoulder at a distance of 0.2 m from the monitor. Participants performed 8 different movements, assigned the number displayed next to each starting position, with green arrows marking the forward and blue the backward movements. Infrared markers (illustrated by red asterisks) were attached to the shoulder, elbow, and wrist joints. The shoulder ( $\theta_s$ ) and elbow ( $\theta_e$ ) joint angles are marked. The arm was held parallel to the horizontal monitor surface and the hand moved within that horizontal plane.

#### Participants.

We tested 12 participants (8 female; 4 male; mean age = 25.67 yr; SD = 3.80; age range: 22-35, mean height = 1.72 m; and mean weight = 65.2 kg) who self-reported to be right-handed and who performed the task with their right arm (Fig. 1). One participant's data were excluded due to failure to successfully complete sufficiently many trials (see *Analysis*). The experiment was approved by the institutional ethics committee, and participants gave written consent. Participants were compensated with 10 euros for the 1-h experimental session.

#### Material.

The experiment was controlled and analyzed in Matlab R2018a making use of the Psychophysics Toolbox Version 2 (PTB-2) for the visual presentation of the movement targets on the horizontally orientated  $110 \times 62$  mm computer screen. A VisualEyez Motion Capture system (Phoenix Technologies Inc.) captured the arm's configuration based on single chip LED markers fixed to four locations on the arm (Fig. 1, note that 2 markers on the splint are represented by a single asterisk representing the computed position of the wrist). The LED markers emit strobe infrared light at a frequency of 4,340 Hz and are detected by two trackers installed on the wall above the display table, each equipped with three infrared cameras. The four markers were sampled at a rate of 250

Hz, and their positions were recorded with visualEyez software.

#### Task.

Movements were instructed by displaying the initial hand position as a red circle on the horizontal computer screen and displaying the target hand position as a green circle (circle radius of 34 mm). All possible initial and target positions and the eight possible movements are shown in Fig. 1. Six movements (*3* to 8) had an amplitude of 25 cm, and two movements (*1* and *2*) had an amplitude of 40 cm, the latter chosen to match the movement conditions used in Ref. 8.

Movement time was imposed by an auditory metronome. During training trials, the metronome repeated the start and end sound (750 and 550 Hz) three times followed by one tone (620 Hz) that indicated movement initiation. The interval between the tones was the desired movement time (400 ms for the fast condition and 800 ms for the slow condition). In the test trials, the metronome played the start tone and the initiation tone once.

#### Procedure.

The experiment consisted of a calibration block and two blocks at the two movement speeds. In the calibration block, the marker positions were registered when the hand was at each of the seven target locations and when the arm was in three different joint angle configurations (arm extended forward and sideways, elbow bent at a right angle). The calibrated hand position for each target was used to verify that the participant's hand was positioned over the correct starting location at the beginning of each trial in the other blocks. The purpose of the calibration of the three joint configurations was to ensure that the calculated joint angles matched the real angles.

The second and third blocks were each organized into 5 sessions of 32 trials each. A session began with a repetition of each movement with the metronome for training. Then, movements were performed without metronome, in random order, with 3 repetitions of each movement. In total the participants completed 320 movement trials, with 160 trials in each condition.

#### Analysis.

Only trials whose movement duration did not exceed the median movement duration of each participant by more than one-third were considered successful and analyzed further. If more than four trials of one movement had to be thus discarded, the participant was excluded from the analysis, which happened for the thirteenth participant.

Movement duration was defined as the time from movement onset to movement offset. Movement onset was defined as the first point in time at which both hand velocity was larger than 5% of peak velocity and hand acceleration was larger than 5% of maximal acceleration. Movement offset was defined analogously. This double criterion was chosen to better deal with the two different movement durations.

Trajectories were trimmed to the interval from on- to offset, filtered with a third-order low-pass Butterworth filter with a cut-off frequency of 5 Hz, and time normalized across all repetitions of each movement and speed condition. Marker positions were shifted so that the shoulder was at [0,0]. The joint angles ( $\theta_j$ ,  $j = \{s, e\}$ ) were estimated from the marker positions as illustrated in Fig. 1. Joint angle velocities and accelerations were computed for the original trajectories but also represented in time normalized form.

The time-normalized joint angle trajectories were used to calculate mean trajectories by averaging across trials, thereby obtaining 16 trajectories (8 movements at 2 speeds) for each participant. These mean trajectories were used to estimate the descending activation and simulate the movements.

For one participant, we performed the estimation and validation procedures (see *Estimation Method*) for each individual trial. This served to assess if the potential inconsistency of the mean trajectories with the kinematic constraints of the arm's geometry could lead to discrepancies. We used the descending activation patterns estimated for each individual trial to predict the individual trial's kinematics from the model. These predictions were averaged across trials and compared to the predictions obtained from the estimates that were based on the mean trajectories. We found that the difference between predicted trajectories was negligibly small and that the estimated activation patterns do not differ notably. We concluded that an analysis based on mean trajectories is appropriate.

#### **Estimation Method**

#### Model.

Estimation of descending activation patterns was based on a model of the biomechanics, muscle dynamics, and the stretch reflex illustrated in Fig. 2. This model was adapted from the well-known model of Gribble and colleagues (8), which is itself a simplification of modern Hill-type muscle models (12) and more complete reflex models (7). We chose the Gribble et al. (8) model as a basis for estimation because it provides benchmark simulations that have previously been compared to experimental data. Because this model



**Figure 2.** Sketch of the model used for estimation of descending activation patterns. Adapted from Ref. 8, the model comprises a reflex, muscle, biomechanical, and sensor component. The input to the model is descending activation, u(t). The output of the model is the predicted joint trajectories  $\theta(t)$ ,  $\dot{\theta}(t)$ .

was also used in our earlier effort to estimate descending activation from optimality principles (9), we will be able to assess the proposed estimation procedure against those earlier results. Moreover, the simplified model lends itself to analytical inversion, enabling us to take observed movement trajectories and directly compute estimated descending activation patterns.

The reflex model combines descending activation, u(t), with the sensory signal, s(t), to generate muscle activation, A(t):

$$A(t) = [u(t) + s(t)]^{+} \text{ for } [x]^{+} = \begin{cases} x \text{ if } x > 0\\ 0 \text{ if } x \le 0 \end{cases}$$
(1)

The model of the sensory feedback signal, s(t), entails a delay, d = 25 ms, over the physical muscle length, l(t), and its rate of change,  $\dot{l}(t)$ :

$$s(t) = l(t-d) + \mu \dot{l}(t-d)$$
 (2)

where the parameter  $\mu = 60$  ms was chosen to remain overall close to a critically damped system. In the model, muscle length, l(t), is determined from the associated joint angle,  $\theta(t)$ , as

$$l(t) = c + c'\theta(t) \tag{3}$$

in which the lever arm, c', is approximated as being constant.

The muscle model was adapted from Ref. 8 and includes three serial components. First, a graded measure of muscle force,  $\tilde{M}(t)$ , reflects the dependence of muscle force on graded motor neuron recruitment:

$$\widetilde{M}(t) = \rho[\exp(zA(t)) - 1] \tag{4}$$

Here, the magnitude parameter,  $\rho$ , is estimated by Gribble et al. (8) from empirical measurements of the physiological cross-sectional area and is specific to each muscle. The form parameter, *z*, is associated with the gradient of motor neuron recruitment and is assumed equal for all muscles.

The second component reflects the calcium kinetics of force generation, modeled as a critically damped harmonic oscillator that low-pass filters (at a time scale of  $\tau = ms$ ) the graded muscle force,  $\tilde{M}(t)$ , to generate the instantaneous muscle force, M(t):

$$\tau^2 \ddot{M} + 2\tau \dot{M} + M = \widetilde{M(t)}.$$
 (5)

Third, the resulting muscle force F(t) depends on the rate of change of muscle length,  $\dot{l}(t)$ 

$$F = M[f_1 + f_2 \arctan(f_3 + f_4 \dot{l})]$$
(6)

with parameter values for  $f_{1-4}$  adopted from Gribble et al. (8) [which were based on physiological data from the cat soleus muscle (13)].

To enable analytical inversion, this muscle model is simplified over the model of Gribble et al. (8) in four ways: 1) muscle lever arms are approximated as constants; 2) muscle parameters, *c*, *c'*, and  $\rho$ , are assumed symmetric across flexors and extensors:  $c'_{iF} = c'_{iE}$ , where the index *i* stands for elbow (*e*) and shoulder (*s*), respectively, and subscripts *F* and *E* refer to flexor and extensor, respectively; 3) passive elastic contributions to muscle force are neglected; and 4) the contributions of biarticulatory muscles are neglected.

This last approximation was necessary to reduce redundancy. The original model included six muscles for the planar elbow-shoulder arm (Fig. 1), two monoarticulatory muscles for each joint, and two biarticulatory muscles. Joint torques thus did not uniquely determine muscle forces. Analytical inversion was not possible for such a redundant system. Neglecting biarticular muscles implies that estimates from analytical inversion are better for movements to which biarticulatory muscles contribute little (e.g., movements of the hand toward or away from the body (*movements 3* to *8* in Fig. 1). All other simplifications are relatively minor assumptions.

The biomechanical model

$$\begin{bmatrix} T_s \\ T_e \end{bmatrix} = \begin{bmatrix} I_{11} & 0 \\ 0 & I_{22} \end{bmatrix} \begin{bmatrix} \ddot{\theta}_s \\ \ddot{\theta}_e \end{bmatrix} + \begin{bmatrix} C_{11} & C_{12} \\ C_{21} & 0 \end{bmatrix} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix}$$
(7)

entails the active joint torques at the shoulder,  $T_s(t)$ , and elbow,  $T_e(t)$ , computed from the flexor,  $F_{iF}(t)$ , and extensor,  $F_{iE}(t)$ , muscle forces:

$$T_{i}(t) = c'_{iE}(F_{iF}(t) - F_{iE}(t))$$
(8)

where  $i \in \{\text{shoulder, elbow}\}$ . The dependence of the Coriolis matrix,  $C(\theta, \dot{\theta})$ , and inertial matrix,  $I(\theta)$ , on joint angles and velocities is listed, e.g., in Ref. 11.

#### Model inversion.

This model thus takes the descending activation, u(t), as input and returns the joint angle trajectories,  $\theta(t)$ , as output. The goal of our estimation method is to invert the model by taking measured joint angle trajectories,  $\theta(t)$ , as input and returning descending activation signals, u(t), that would generate these joint trajectories according to the model. The estimated descending activation signal, u(t), can be directly compared to the estimated time course of muscle activation, A(t), to assess the contribution of reflex-induced muscle activation.

Even though we are neglecting biarticulatory muscles, we are still left with descending activation signals for four muscles based on only two joint angles. This remaining muscle redundancy is due to potential cocontraction of flexor and extensor muscles around the same joint. We address this redundancy by making and varying assumptions about the level of such cocontraction. To enable this approach, it is convenient to transform descending activation signals, u(t), into reciprocal, R(t), and cocontraction, C(t), signals:

$$R_i(t) = (u_{iF}(t) - u_{iE}(t) + c_{iF} - c_{iE})/(2c'_i)$$
(9)

$$C_i(t) = (u_{iF}(t) + u_{iE}(t) + c_{iF} + c_{iE})/(2c'_i)$$
(10)

C captures the mean descending activation signal sent to extensor and flexor, while R captures the difference between descending activation signals sent to the two antagonistic muscles.<sup>1</sup>

The first step in the inversion is an inverse biomechanical dynamics, computing from given joint trajectories and their derivatives the active joint torques,  $T_i(t)$ , via *Eq.* 7. These can

<sup>&</sup>lt;sup>1</sup>These notions were originally proposed within equilibrium point theory (10), which interprets descending activation as a virtual length,  $\lambda = -u$ , at which the combination of descending activation and sensory feedback reaches threshold:  $u + s = -\lambda + \text{length} = 0$ . This makes it possible to interpret *R* and *C* in spatial terms. Our analysis does not profit from that interpretation, so we do not invoke it here.

be linked to muscle forces,  $F_{iF}$  and  $F_{iE}$ , via Eq. 8. Substituting muscle forces by instantaneous muscle forces via Eq. 6 leads to

$$\frac{T_i(t)}{c'_{iE}} = M_{iF}(t)a_{iF}(t) - M_{iE}(t)a_{iE}(t)$$
(11)

with the abbreviations

$$a_{iF}(t) = f_1 + f_2 \arctan(f_3 + f_4 \dot{l}_{iF}(t))$$
(12)

$$a_{iE}(t) = f_1 + f_2 \arctan(f_3 + f_4 \dot{l}_{iE}(t))$$
(13)

To replace instantaneous muscle forces, M(t), by graded muscle forces,  $\tilde{M}(t)$ , we need to solve the Calcium dynamics *Eq.* 5:

$$M(t) = \frac{1}{\tau^2} \int_{-\infty}^{t} (t - t') e^{-(t - t')/\tau} \widetilde{M}(t') dt'$$
(14)

This is the stationary solution. As in all previous uses of this model, transients are assumed to have decayed. This solution can be well approximated by a pure delay:

$$M(t) \approx \widetilde{M}(t - \tau) \tag{15}$$

To understand this, it is useful to note that for  $\tau \rightarrow 0$ , the integral kernel in *Eq.* 14 approaches the Dirac Delta-function,  $\delta(t - \tau)$ . Figure 3 illustrates that at relevant parameters settings, M(t) obtained from *Eq.* 5 is essentially just delayed by

$$\tau = 15 \text{ ms over} \widetilde{M}(t)$$
. This approximation makes it possible to substitute  $M(t)$  and then  $\widetilde{M}$  by muscle activation,  $A$ , via Eq. 4

$$\frac{T_j(t)}{c'_{iE}\rho_i} + a_{iF}(t) - a_{iE}(t) = a_{iF}(t)\exp\left(zA_{iF}(\widetilde{t})\right) - a_{iE}(t)\exp\left(zA_{iE}(\widetilde{t})\right)$$
(16)

where  $\tilde{t} = t - \tau$ .

The last step is to use the reflex model, Eq. 1, to replace the muscle activation, A, by descending activation, u, and sensory signals, s:

$$\frac{T_{j}(t)}{c_{iE}'\rho_{i}} + a_{iF}(t) - a_{iE}(t) = a_{iF}(t)\exp\left(z\left[u_{iF}(\tilde{t}) + s_{iF}(\tilde{t})\right]^{+}\right) - a_{iE}(t)\exp\left(z\left[u_{iE}(\tilde{t}) + s_{iE}(\tilde{t})\right]^{+}\right)$$
(17)

These two equations  $(i \in \{\text{shoulder, elbow}\})$  determine only two of the four descending activation signals,  $u_{iF}$  and  $u_{iE}$ . We use *Eqs. 9* and *10* to reduce these four variables to the two reciprocal signals,  $R_i(t)$ , while selecting fixed values or fixed time courses for the cocontraction signals,  $C_i$ .

Analyzing the semilinear threshold function,  $[\cdot]^+$ , separately for positive and negative arguments leads to four cases. When both arguments are negative, the equations do not depend on *R* and no estimate is possible. Straight-forward algebra delivers solutions for the three other cases, leading to

$$R_{i}(t) = \begin{cases} \text{undefined} & \begin{cases} \text{if } u_{iF}(\tilde{t}) > s \\ \text{and } u_{iE}(\tilde{t}) > s \\ \text{and } u_{iE}(\tilde{$$

The following abbreviations are used:

$$\eta(t) = \frac{T_j(t)}{c'_{iE}\rho_i} + a_{iF}(t) - a_{iE}(t)$$
(19)

$$h_i(t) = \theta_i(\hat{t}) + \mu \dot{\theta}_i(\hat{t})$$
(20)

$$d_{iF}(t) = a_{iF}(t) \exp(zc'_{iE}(C_i - h_i(t)))$$
(21)

$$d_{iE}(t) = a_{iE}(t) \exp(zc'_{iE}(C_i + h_i(t)))$$
(22)

where  $\hat{t} = \tilde{t} - d = t - \tau - d$ . Note that the case conditions themselves depend on the to be estimated descending activation signals,  $u_{iF}$  and  $u_{iE}$ . To address this, the algorithm of

$$\begin{cases} \text{if } u_{iF}(\tilde{t}) > s(\tilde{t}) \\ \text{and } u_{iE}(\tilde{t}) > s(\tilde{t}) \\ \text{if } u_{iF}(\tilde{t}) < s(\tilde{t}) \\ \text{and } u_{iE}(\tilde{t}) < s(\tilde{t}) \\ \text{and } u_{iE}(\tilde{t}) > s(\tilde{t}) \\ \text{and } u_{iE}(\tilde{t}) > s(\tilde{t}) \\ \text{and } u_{iE}(\tilde{t}) > s(\tilde{t}) \end{cases}$$

$$(18)$$

estimation computes  $R_i(t)$  for all three cases at every moment in time. The resultant values are combined with the assumed values for  $C_i$  to determine  $u_{iF}$  and  $u_{iE}$  via Eqs. 9 and 10. We then do a consistency test by comparing the values of *s* and *u* and checking whether the estimated *u* values indeed lie within the range of their respective case. Only the selfconsistent estimates where *u* falls within that range are retained. Empirically, at almost every moment in time, only one estimate is found that is self-consistent, leading to a unique estimate (see below). The transition of estimates from one case to another is also continuous, which leads to the smooth trajectories for *u* (see Figs. 8 and 9).

#### Validation methods.

We applied the estimation method for a set of different cocontraction signals,  $C_i(t)$  ( $i \in \{\text{shoulder, elbow}\}$ ). To probe



**Figure 3.** An example simulation illustrates how M(t) and M(t) relate. These time courses were obtained by estimating the descending activation pattern for the third movement and then predicting the time courses of M(t) and  $\widetilde{M}(t)$  by simulating the complete model, using the exact form of Eq. 5. The shoulder flexor muscle forces [instantaneous force, M(t), in red; graded muscle force,  $\widetilde{M}(t)$ , in light red); and the extensor muscle forces (M (t) in blue;  $\widetilde{M}(t)$  in light blue] are shown. The time measurements marked by the black dots illustrate the time delay between the 2 curves.

the extent to which higher levels of cocontraction enable fast movements (8), we tested time invariant levels of  $C_i$  from 0.2 to 1.0 rad. The time-varying stiffness measures reported in Ref. 14 motivated a set of different ramp-like time courses for cocontraction that we also tested. For each set of  $C_i$  values or trajectories, we estimated the  $R_i(t)$  trajectories and computed the descending activation signals,  $u_{iF}(t)$  and  $u_{iE}(t)$ , for the ensemble of data sets obtained in the behavioral experiments (see *Model inversion*).

We then used these descending activation signals as input to the model, numerically simulating the sampled movements. The consistency of the estimate was assessed by comparing the predicted hand trajectories,  $(\hat{X}, \hat{Y})$ , to the experimental ones, (X, Y), using the root-mean-square error (RMSE)

$$\text{RMSE} = \frac{100}{TA} \sum_{j=1}^{N} \sqrt{\left(\hat{X}(t_j) - X(t_j)\right)^2 + \left(\hat{Y}(t_j) - Y(t_j)\right)^2}$$
(23)

where both time series are sampled by the same number, T, of time steps,  $t_j$ . The error was normalized across movements by dividing by movement amplitude, A.

# RESULTS

#### **Kinematics of the Human Movement Data**

Movement time approximately matches the duration specified by the metronome with a mean movement time across all movements and participants of 779 ms (SD = 32 ms) in the slow and 445 ms (SD = 22 ms) in the fast condition (Table 1).

The kinematics of the movement data are consistent with literature data (11). In both the fast and the slow movement conditions, hand paths are relatively straight (Fig. 4).

Figure 5 shows that hand trajectories are smooth and hand velocity profiles are approximately bell shaped. The two movements with larger amplitude (1 and 2) reach a higher peak velocity. The velocity profiles are slightly asymmetrical, rising more steeply and falling more slowly, as is typical of timed and targeted movements.

Figure 6 gives a sense of the variability of the human movements by plotting the hand's velocity (the length of the

hand's velocity vector) as a function of normalized time for all trials of one participant.

#### Validation of Estimation

The self-consistency of the estimation of descending activation was assessed by comparing observed movement kinematics to the movement kinematics predicted from the model based on the estimated descending activation patterns. Table 2 shows the mean RMSE for the hand's trajectory across the eight movements. Overall, the mean RMSE was 1.3% in the slow condition and 2.3% in the fast condition, both expressed as a proportion of the amplitude of the movement. This difference was significant. Note that RMSEs are larger for the two longer *movements 1* and 2, and relatively invariant across the six shorter movements (3 to 8).

Visual inspection of the predicted kinematics shows that the estimate captures a number of qualitative features of the human movement kinematics (Figs. 4 and 5). Note that differences between different movements (from dark red to orange in Figs. 4 and 5) are captured by the estimates (from dark blue to light blue). The asymmetry of velocity profiles is also captured by the estimates.

Figure 6 provides an intuition for how predictions derived from individual trials match these trial characteristics. Figure 6 also illustrates the considerable variability of the human movement data, especially in the fast condition, that is adequately captured by the estimates.

#### **Temporal Structure of Descending Activation**

We first examine the descending activation patterns estimated for a constant C signal of 0.55 rad. We may look at these descending activation patterns in two ways. The first is based on the R signal of Eq. 9, which can be directly compared to movement kinematics. To facilitate that comparison, we transformed the R signal into hand space by treating it as a joint angle and applying the geometrical model. The time course of the hand's spatial position along a line connecting the initial to the target position is shown in Fig. 7 together with the transformed R signal projected onto that same line. Time is normalized, so that the scaling of slow (Fig. 7, *left*) versus fast (Fig. 7, *right*) movements is directly visible. For slow movements, the R signal is monotonic and similarly shaped as the hand trajectory but advanced in time. This reflects the delay (or phase shift) between descending activation and movement caused by muscle and biomechanical dynamics. For fast movements, the R signal

**Table 1.** Movement time and its standard deviationacross participants for each of the eight movements inthe two movement conditions, slow vs. fast

		Movement										
Condition	1	2	3	4	5	6	7	8				
Slow												
<i>MT</i> , ms	798	791	809	755	717	694	809	855				
MT <sub>SD</sub> , ms	25	18	30	23	18	19	19	19				
Fast												
<i>MT</i> , ms	455	448	460	443	400	495	482	479				
MT <sub>SD</sub> , ms	25	18	30	23	18	19	19	19				

MT, movement time;  $MT_{\rm SD}$ , movement time standard deviation.

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**Figure 4.** The hand paths are plotted for the 8 different movements in the slow (A) and fast (B) conditions. Experimental data (averaged across trials and participants) are in shown red, with the dashed line indicating the backward movement. Predictions from the estimated descending activation (based on *C* signal = 0.55 rad) are shown in blue.

is not simply rescaled but has a qualitatively different temporal structure. It is nonmonotonic and initially is strongly advanced in time over the hand trajectory, while it falls below the hand trajectory at the end of the movement for the two longer movements (1 and 2, rows 1 and 2).

The second way to look at the descending activation pattern is to do so directly in the activation space. This makes it possible to compare the descending activation pattern to muscle activation and relevant joint torques. This is done in Fig. 8 for the shoulder and in Fig. 9 for the elbow joint. Three observations are useful. First, interaction torques are larger for fast movements (solid lines) and their time structure differs in some cases compared to slow movements (dashed). Second, muscle activation starts from an initial level and returns to that same level at the end of the movement, similar to interaction torques. Muscle activation is larger for fast (solid lines) than for slow (dashed lines) movements. Its temporal structure differs qualitatively across the two speeds. For fast movements, there are cases in which muscle activation drops below the initial and final level during the movement. Third, descending activation signals are initially aligned with muscle activation (up to ~15 to 20% of movement time) but then become qualitatively different from the



Figure 5. Hand kinematics for the slow (A, C, and E) and the fast condition (A, D, and F) shown as functions of normalized time. Human data averaged over participants and trials are plotted in different shades of red for the 8 different movements. Overlaid are the predictions from the estimated descending activation signals in different shades of blue (estimates based on C signal = 0.55). The ordering of predicted kinematics from dark blue to light blue is aligned with the ordering of experimental kinematics from dark red to orange. A and B: hand position along the vector pointing from start to target. C and D: hand position orthogonal to that vector. E and F: hand velocity along the instantaneous movement direction.



**Figure 6.** Individual trial hand velocity profiles for the slow (*left*) and fast (*right*) movement condition. *Top*: data from 1 participant. The 8 different movements are indicated by different colors. Movement time is normalized across all movements and trials. *Bottom*: model predictions generated from estimates of descending activation for each individual movement of the participant.

initial level. The temporal structure of descending activation for fast movements (solid) is qualitatively different from that of slow movements (dashed), with a tendency to advance over the time course estimated for slow movements early in the movement and then realign with that time course late in the movement.

The dependence of the estimated descending activation pattern on the assumed levels or time courses of cocontraction, *C*, was examined systematically (Figs. 10 and 11). For an exemplary movement and joint, results are shown in Fig. 10. In Fig. 10, A-D, the level of time-invariant cocontraction is varied within a range that may be considered physiologically plausible (8). The time structure of the estimated *R* signal depends on the assumed level of cocontraction. It is most strongly modulated for weak cocontraction (light gray). Even at the strongest level of cocontraction (dark gray), however, the time course of the *R* signal differs qualitatively between slow and fast movement and includes nonmonotonic components. Intermediate levels of cocontraction show the weakest temporal structure of the *R* signal for the fast

 Table 2. RMSE is expressed as percentages of movement amplitude

		Movement										
Condition	1	2	3	4	5	6	7	8				
Slow	2.1	1.7	0.9	1.0	1.3	1.1	1.4	1.0				
Fast	3.5	3.2	1.8	2.0	1.9	2.2	2.4	1.9				

Root-mean-square error (RMSE) is averaged across participants and across the different constant C signals used in the estimation. RMSE across the 8 movements and the 2 movement conditions are listed, slow vs. fast. movement. This is the level we used in our previous analysis (C = 0.55 rad).

Would a temporal modulation of cocontraction reduce the temporal complexity of the *R* signal? We compared four types of modulation within the midrange of *C* levels as illustrated in Fig. 10*E*: constant (solid), increasing (dashed), maximum in the middle of the movement (dotted), and a superposition of increasing with a maximum in the middle of the movement (dash-dotted). The *R* estimates vary very little when these different time courses of *C* are imposed (Fig. 10*F*). In all cases, the validity of the estimate is unaffected by the variation of the *C* signals as observed (red) and predicted (blue) joint trajectories remain close (Fig. 10, *C*, *D*, and *G*).

We defined a measure, *N*, of how strongly the *R* signal is temporally structured by computing the mean squared difference between the *R* signal and a linear ramp from initial to target level. The linear ramp was assumed to reach its final position at the point in time when peak hand velocity is reached to be consistent with experimental findings (15). This measure is larger, overall, in the fast versus the slow condition across all movements and joints (Fig. 11). For the shoulder (Fig. 11, *top*), the measure decreases with higher levels of cocontraction. For the elbow (Fig. 11, *bottom*), this decrease is only apparent in the fast condition. This may be a bottom effect, as the measure of temporal modulation is much smaller for the elbow than for the shoulder.

We tested if the difference between the two speed conditions was significant by conducted *t* tests for the two joints at a level of C = 0.55 rad. All tests were significant with a smaller mean in the slow condition: elbow:  $N_{\text{fast}} = 0.11$  rad,  $N_{\text{slow}} = 0.06$  rad (P = 2.29, e - 05); shoulder:  $N_{\text{fast}} = 0.20$  rad,  $N_{\text{slow}} = 0.10$  rad (1.72 e - 05) at a 1% significance level.



**Figure 7.** The coordinate of the hand's position along the line connecting initial to target position is plotted as a function of time for all 8 movements (*rows 1–8*) in the slow (*left*) and fast (*right*) conditions. Human data averaged over participants and trials are shown in red, and the data predicted from the estimates of the descending activation pattern (at a C signal = 0.55 rad) are shown in blue. The *R* signal transformed into hand space and projected onto the same lines is shown in gray.

# DISCUSSION

In this study, we used a simple model of the stretch reflex and the muscle and biomechanical dynamics to directly estimate the descending activation patterns that would have generated observed human movements. The classical setting of planar human arm movements with two degrees of freedom was used at two imposed movement times. This provided the opportunity to examine if descending activation patterns vary with movement speed in ways that go beyond mere rescaling.

Three major findings emerged. First, descending activation begins to deviate from muscle activation after about 20% of movement time, and, unlike muscle activation, does not return to its initial level. Second, descending activation is temporally structured in a way that may be nonmonotonic and that does not simply rescale with movement time. Third, if the level of cocontraction is kept at different timeinvariant levels within a movement, the estimated descending activation pattern has a different temporal structure. Below we discuss these three insights in turn and then assess the estimation procedure itself.

#### **Descending Activation versus Muscle Activation**

When movement is initiated, muscle activation is largely driven by descending activation. In Figs. 8 and 9, the time courses of these two signals, if shifted to start from the same level, develop identically in this first phase. They begin to deviate when between 15 and 20% of movement time has passed. This is when the reflex begins to contribute to movement muscle activation. Although we cannot exclude that the exact time window depends on the specific model, this is an intriguing way to observe this onset.

The deviation between descending and muscle activation continues throughout the movement. In fact, descending activation settles on a final level that is far from the initial level, while muscle activation returns to its initial level. Except for changes in cocontraction or changes relative to gravity not treated here, muscle activation would generally return to initial levels.

The terminal difference between descending and muscle activation is natural and reflects the posture-movement problem: if descending activation did not change over the movement, the stretch reflex would work against the shift in



**Figure 8.** Time courses of interaction torques, descending activation, and muscle activation for the shoulder joint for the 8 different movements (*rows 1–8*). *Left*: shoulder interaction torques for the fast (solid) and the slow (dashed) condition. *Middle*: descending activation, *u(t)* (blue), and muscle activation, *A(t)* (red), for the shoulder flexor muscle (fast condition: solid, slow condition: dashed). Activations were shifted to start at 0 to enable visual comparison with muscle activation. *Right*: same for the shoulder extensor muscle.



posture brought about by the movement (16). Supportive evidence comes from force-field adaptation studies that detected shifts in the end state even when force fields were zero there, which was interpreted as indicative of a path-integrated component to the motor command (17).

#### **Time Course of Descending Activation**

For slow movements, the estimated descending activation has, in most cases, a monotonic "ramp," like a time course that terminates near the time of peak velocity. The ramp shape is broadly consistent with the equilibrium point interpretation of movement generation (10) and the termination time is consistent with earlier experimental estimates of the timing of descending activation (15). Not all slow movements exhibit this simple shape of descending activation, however.

Purely kinematic conceptions of movement generation such as the equilibrium point hypothesis predict that descending "motor commands" are merely rescaled in time when movement duration varies. The time course of the estimated descending activation pattern is not consistent with such rescaling. This is obvious in Figs. 8 and 9, in which time is normalized across the two duration conditions. For most movements, descending activation patterns for fast movements deviate from those of slow movements through extra peaks or troughs early in the movement. This speaks against a purely kinematic conception of movement generation.

Overall, the time courses of the estimated descending activation patterns are not very complex. They could be construed as consisting of a rescaled kinematic component that would reflect the shifting posture in the manner of equilibrium point thinking and a superposed movement command that does not rescale and starts and ends at zero. This second component would then address the nonlinearities of movement generation including interaction torques (shown in Figs. 8 and 9) (18). The second component would be responsible for generating sufficient initial muscle activation to accelerate the joint, the intuition behind earlier postulates of an "N shape" of descending signals (19). The time structure of the second component would thus reflect the properties of the motor plant in the manner of the "internal models" of computational theories of motor control (4). This observation is also broadly consistent with the observation that hybrid models that combine control by a shifting equilibrium point with a feed-forward signal directly to the muscle are sufficient to explain fast movements (20).



**Figure 9.** Time courses of interaction torques, descending activation, and muscle activation for the elbow joint for the 8 different movements (*rows 1–8*). *Left*: shoulder interaction torques for the fast (solid) and the slow (dashed) condition. *Middle*: descending activation, u(t) (blue), and muscle activation, A(t) (red), for the shoulder flexor muscle (fast condition: solid, slow condition: dashed). Activations were shifted to start at 0 to enable visual comparison with muscle activation. *Right*: same for the shoulder extensor muscle.

By reinterpreting descending activation as threshold lengths of the stretch reflex, we were able to transform the descending activation patterns into hand space, a purely kinematic transformation. The resulting time courses (Fig. 5) appear more invariant across movements than those in joint space (Figs. 8 and 9). Decomposing these trajectories into a postural component (taken to be the time course for the slow movements) and a movement component suggests that the internal model may not need to capture the details of the muscle level. It may be sufficient to capture the effective dynamics of the plant at the level of the hand in space. Forcefield studies aimed at characterizing the internal model have typically applied forces to the hand rather than to individual joints. In that respect, this conjecture is not inconsistent with that line of work. Note, however, that studies applying perturbations at the joint level have uncovered long-latency reflex contributions that are sensitive to joint configuration (21).

# Time Courses of Descending Activation Depend on Cocontraction

We found that the estimated temporal patterns of descending activation differ when different levels of cocontraction are assumed, even when these are kept constant during the movement (Fig. 10). Thus the same movement can be achieved at different levels of cocontraction by different time courses of descending activation.

At higher levels of cocontraction, the time courses of descending activation are less complex. Increasing cocontraction thus provides a strategy to simplify control. This could be a learning strategy when first exposed to a new movement skill and may be behind the idea of "freezing" degrees of freedom (22).

By varying the level of cocontraction, the effective impedance of a joint can be modulated (23). This plays an important role in the human capacity for compliant control (24). Our finding that different levels of cocontraction require different time courses of descending activation implies that compliance hinges on the capacity of the motor system to generate these different time courses.

#### **Comparison to Prior Work**

The estimation method is essentially an analytical inversion of the model. The model takes descending activation as input and generates movement as output. The estimation takes movement as input and generates descending activation as output. The consistency of the estimate was checked by using estimated descending activation as input to the model to predict the movement. Consistency in that sense was broadly observed across the data set.





Consistency alone does not establish the validity of the model. That model is, of course, neither new (8) nor surprising. Its biomechanical part is exact. The muscle model is a simplification that is qualitatively consistent with Hill-type models. The model of the stretch reflex is very simple and generic. We used this particular model for the estimation method for three reasons.

First, this model is simple enough to enable analytic inversion with only a few further assumptions. Classical Hill-type muscle models (25) are not in any obvious way analytically invertible nor are more complex reflex models (7).

Second, using this model makes it possible to compare the results with those of the original study (8) that had demonstrated that simple, ramp-like descending motor "commands" are sufficient to generate realistic movements. Gribble and colleagues (8) did not report movement time, but the published time courses suggest movement times between 700 and 800 ms consistent with our "slow" condition for which we did estimate "ramp"-like descending activation patterns for most movements. Note, that the earlier study only included movements 1 and 2 of the present study. The apparent discrepancy between the two studies could thus be due to the slow movement times in the earlier work and its limited sampling of workspace.

Third, using this model makes it possible to also compare to our own earlier work (9) in which we estimated descending activation by minimizing its change given movement amplitude and movement time. Our estimates are qualitatively consistent with those earlier estimates. This is significant because the earlier estimate was based on an ad hoc optimality criterion that was recognized as invalid. (The criterion was chosen to make the theoretical point that even when minimizing the deviation from a ramp, nonmonotonic and nonrescaling descending activation profiles result.) The invalidity of the criterion was visible in a failure to predict the asymmetry of hand velocity profiles correctly. Because lengthening muscles generate more force than shortening muscles at the same level of input and the velocity-dependent terms always resist movement (26), breaking can be achieved with less chance of descending activation than accelerating. A minimally changing descending activation principle will thus tend to break hard and accelerate softly, while humans accelerate hard and break softly. The estimation method proposed in this paper captures, in contrast, the asymmetry of human velocity profiles correctly (Fig. 6).

# **Limitations of the Estimation Method**

The inversion of the model for estimation was achieved by analytical computation and is thus, within the set of assumptions, exact. The only serious assumption that goes beyond those shared with Gribble et al. (8) is our neglecting biarticulatory muscles to minimize muscle redundancy. As this assumption was not made in our earlier effort (9), the consistency with those earlier results indicates that the assumption does not cause qualitative error.

A better framing of the assumption is to think of the modeled muscles as "virtual" muscles that lump together the contributions of mono- and biarticulatory muscles. The limitation of this approximation is then that there are movements in which these two muscle groups covary and movements in which they do not. The descending activation patterns would be expected to differ across such movements, reflecting the need to recruit the "virtual" muscles more or less strongly. Such a contrast is expected between the two forward-backward *movements 3* and 4, in which the biarticulatory muscle hardly change length, and the lateral *movements 1* and 2, in which the biarticulatory muscles covary in



length with the monoarticulatory ones. We found no qualitative differences between the time courses obtained for these two groups of movement, suggesting again that the approximation does not lead to major distortions. The analytical approach would not scale well when mus-

cle and reflex models are made more complex. For instance, classical Hill-type models do not appear tractable to analytic inversion. As a consistency check, we fed the descending activation profiles as estimated here into a Hill-type model with the rigid tendon (p. 185 in Ref. 25 using parameters from Refs. 27 and 28: see Supplemental Material S1 for details and results.) We found that such a model generates qualitatively reasonable movements at the two tested speeds.

Including more complex reflex models (29) may not be tractable to analytical inversion either. Most current work with such models invokes ad hoc descending signals to generate qualitatively plausible movement trajectories (7, 30). Systematic model-based estimation of descending activation patterns for such more complex models is highly desirable (31). A numerical approach to model inversion might be feasible, although it may require other assumptions such as regularization terms. The current results based on analytical inversion may provide a useful baseline for such work.

#### Conclusions

We developed a method to estimate descending activation patterns from experimental trajectories by inverting a model

of the stretch reflex and muscle and biomechanical dynamics. We applied the method to a set of experimental trajectories of planar arm movements at two movement speeds.

We found that the stretch reflex contributes substantially to movement generation starting as early as 15 to 20% of movement time. The observed difference between descending and muscle activation was maximal near the end of the movement, reflecting the shift of the stable postural state during movement. Failing to include spinal reflexes in computational models is thus clearly a mistake. For instance, a "neural" signal estimated from optimal feedback control without a model of the stretch reflex (32) does not provide a qualitatively correct estimation of the activation that descends the spinal cord.

We also found, however, that the stretch reflex does not eliminate the need to generate specific time courses for the descending activation patterns. While slow movements tended to be consistent with "ramp-like" descending activation patterns that could be interpreted as graded shifts of equilibrium posture, fast movements do not result from a mere rescaling of these patterns. Instead, fast movements contain a second component in addition to this postural shift that could be thought of as the output of an internal model that reflects the dynamics of the plant. When cocontraction is varied to achieve different levels of compliance, different time courses must generated by such an internal

Figure 11. The measure, N, of how strongly the R signal is temporally structured for the shoulder (top) and elbow (bottom) for all 8 movements, the 2 speeds (slow: blue; fast: red), and 3 levels of constant C signals (0.4, 0.55, and 0.7 rad, light to dark shades of blue/red). SDs are indicated by error bars.



Overall, our direct estimation of the time course of descending activation from observed kinematics revealed both the qualitative and quantitative importance of the stretch reflex as well as time courses of descending activation that are specific to movement speed and levels of compliance as postulated for internal models. This suggests a research program in which numerical estimation techniques could be used to establish descending activation patterns for more realistic muscle models, larger sets of redundant muscles, and more complex reflex models. Our data sampling a large part of workspace at different speeds and our analytical results based on simplified muscle and reflex models may serve as a benchmark for such advanced estimation efforts.

#### DATA AVAILABILITY

The motion data are published at https://doi.org/10.6084/m9. figshare.24968271, and the source code for the experiment and simulation is available at https://gitlab.com/c.hummert/inversedynamics.

# SUPPLEMENTAL DATA

Supplemental Material S1: https://doi.org/10.6084/m9.figshare. 25713270.v1.

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# DISCLOSURES

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

#### AUTHOR CONTRIBUTIONS

C.S.H. and G.S. conceived and designed research; C.S.H. performed experiments; C.S.H. analyzed data; C.S.H., L.Z., and G.S. interpreted results of experiments; C.S.H. prepared figures; C.S.H. and G.S. drafted manuscript; C.S.H., L.Z., and G.S. edited and revised manuscript; C.S.H., L.Z., and G.S. approved final version of manuscript.

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