Proximal Versus Distal Control of Two-Joint Planar Reaching Movements in the Presence of Neuromuscular Noise

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Determining how the human nervous system contends with neuro-motor noise is vital to understanding how humans achieve accurate goal-directed movements. Experimentally, people learning skilled tasks tend to reduce variability in distal joint movements more than in proximal joint movements. This suggests that they might be imposing greater control over distal joints than proximal joints. However, the reasons for this remain unclear, largely because it is not experimentally possible to directly manipulate either the noise or the control at each joint independently. Therefore, this study used a 2 degree-of-freedom torque driven arm model to determine how different combinations of noise and/or control independently applied at each joint affected the reaching accuracy and the total work required to make the movement. Signal-dependent noise was simultaneously and independently added to the shoulder and elbow torques to induce endpoint errors during planar reaching. Feedback control was then applied, independently and jointly, at each joint to reduce endpoint error due to the added neuromuscular noise. Movement direction and the inertia distribution along the arm were varied to quantify how these biomechanical variations affected the system performance. Endpoint error and total net work were computed as dependent measures. When each joint was independently subjected to noise in the absence of control, endpoint errors were more sensitive to distal (elbow) noise than to proximal (shoulder) noise for nearly all combinations of reaching direction and inertia ratio. The effects of distal noise on endpoint errors were more pronounced when inertia was distributed more toward the forearm. In contrast, the total net work decreased as mass was shifted to the upper arm for reaching movements in all directions. When noise was present at both joints and joint control was implemented, controlling the distal joint alone reduced endpoint errors more than controlling the proximal joint alone for nearly all combinations of reaching direction and inertia ratio. Applying control only at the distal joint was more effective at reducing endpoint errors when more of the mass was more proximally distributed. Likewise, controlling the distal joint alone required less total net work than controlling the proximal joint alone for nearly all combinations of reaching distance and inertia ratio. It is more efficient to reduce endpoint error and energetic cost by selectively applying control to reduce variability in the distal joint than the proximal joint. The reasons for this arise from the biomechanical configuration of the arm itself. [DOI: 10.1115/1.4006811]

Keywords: reaching, motor control, neuronal noise, energy, proximal, distal, redundancy

1 Introduction

Reaching is a very elementary task. However, it requires sophisticated control to overcome several fundamental challenges during movement. One of the most significant of these challenges is inherent neuromuscular noise. This noise emanates from both internal neuromuscular signals and external sources [1,2]. Numerous control theories have attempted to explain how humans compensate for motor noise during movement [3–7]. Experimental studies at the muscle level have shown how increased co-contraction of shoulder [8] or elbow muscles [9] could be used to strategically minimize noise without compromising endpoint accuracy. Applying control to reduce the negative impacts of noise involves expending control effort (i.e., energy). The human nervous system must therefore decide how to most effectively

apply control across the joints involved in any task in such a way as to maximize performance outcome, while also limiting the total energy expended. For the task of planar reaching, there are specific dynamic interactions between the torques applied at the shoulder and elbow [10,11] and these will also vary depending on the movement direction. It is not known how this biomechanical coupling influences how motor noise independently applied at each joint affects performance accuracy or the effectiveness of any control effort that is applied at either joint. Therefore, the purpose of this study was to determine how such biomechanical factors (arm configuration and differences in reaching direction) influence how different combinations of motor noise and/or control applied at each joint in turn affect reaching accuracy and the energetic cost of reaching.

Noise and control at the proximal and distal joints may affect the dynamics and coordination of goal-directed movements differently [12–15]. For example, experiments suggest that people may first assert proximal joint control, followed by distal joint control, to help them learn new skilled tasks [13,15]. McDonald [15] demonstrated in a dart throwing task that, with practice, the variability

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at the distal joints decreased and the cross-joint correlations between the distal and proximal joint also decreased. They suggested that people could adopt a control strategy of *freeing* and *freezing* different degrees of freedom in the system to learn this new task. Likewise, when using an experimentally controlled playing form, joint kinematics of novice violinists were more variable than those of experts [14]. However, as the novices practiced over time, variability at the distal joints decreased and approached the behavior exhibited by expert violinists. These experimental observations suggest that task performance may be more sensitive to controlling variability at distal joints than proximal joints. However, one cannot easily infer the nature of the underlying control process simply by observing the structure of the variability in the observed behavior [16]. A computational framework is required to independently manipulate the biomechanical and control factors and then measure their effects on task performance.

Understanding how the central nervous system regulates and structures movement variability is critical to understanding how humans perform skilled movements [1,17–20]. Trial-to-trial variability in most movement tasks is, in fact, *not* entirely random, but is structured in specific ways that have important implications for control [17–20]. Geometry-based approaches to analyzing the structure of variability in experimental data [21–23] have provided some insights into these issues. However, these approaches inherently ignore the question of how the biomechanical structure of the system performing the task (e.g., the arm, etc.) can themselves create structure in the measured task performance [16]. In fact, observed movement variability could be structured for any of *several* reasons *not* related to controlling the task itself [16]. These might include the biomechanical structure of the system, the signal-dependent nature of neuromuscular noise, or a desire by the nervous system to satisfy other task goals such as minimizing fatigue or exploring alternative control strategies. Theoretical approaches that tie these ideas to stochastic optimal control theory [17,19,20] provide a more concrete computational framework for properly interpreting the specific control implications of such experimental observations [16,24,25]. These concepts have not yet been applied to specifically address the question of how the nervous system might partition control across proximal versus distal joints in specific goal-directed tasks. Thus, it is not yet known precisely how integrating distal and/or proximal control minimizes the effects of noise on task performance. Experimentally, one cannot manipulate these factors independently to separate the roles of distal versus proximal noise and/or control on task performance. A rigorous computational analysis is needed to investigate the distinct functions of distal and proximal joints during movement.

Here, we used a 2 degree-of-freedom torque driven arm model to generate point-to-point reaching movements to fixed targets. We varied both the movement direction and the inertia distribution along the arm to determine how these biomechanical factors impacted task performance. We then applied noise and feedback control in varying combinations at each joint torque. First, we examined how, in the absence of any additional control, adding *noise* to either the distal (elbow) or proximal (shoulder) joint torques independently affected the endpoint errors and total net work. We hypothesized that, in the absence of any feedback control, performance in this reaching task would be more sensitive to distal (elbow) noise than to proximal (shoulder) noise. We also hypothesized that these effects would be strongly influenced by biomechanical factors (i.e., reaching direction and/or inertial properties).

Second, we quantified how, when noise was present at *both* the elbow and shoulder joint torques, applying feedback *control* to either the elbow joint torque, or shoulder joint torque, or both, affected the endpoint errors and total net work. Because we imposed reaching movements where the kinematics were fully specified, this yielded a one-to-one mapping from hand kinematics to joint torques. This then removed any *kinematic* redundancy in the system and, thus, also any joint *torque* redundancy for the nominal (noise-free) movements themselves. However, there was redundancy in terms of where to apply *control* (i.e., at which joint torque), since the controller had the choice of applying limited control resources to reduce the effects of the applied noise either at the shoulder, or at the elbow, or both. Here again, geometry-based methods [21–23] that consider only kinematic redundancy cannot address this important question. Here, we hypothesized that when noise was present at both joints, applying only distal (elbow) control would be more effective than applying only proximal (shoulder) control for maximizing task performance. We also hypothesized that these effects, such as those previously discussed, would also be strongly influenced by biomechanical factors (i.e., reaching direction and/or inertial properties).

2 Methods

2.1 Arm Model. A planar 2 degree-of-freedom (dof) torque-driven model of the right arm (Fig. 1) was developed. This model was designed to specifically address how the biomechanics of the arm and the reaching task influences the options any controller might have to exploit *control redundancy* at the joint torque level. As with any model, this model represented a simplification from the true biological system. For example, our model did not include a wrist joint. Experimentally, humans exhibit minimal net torques and very little movement at the wrist [26]. Thus, many studies have used similar 2-joint models to simulate planar arm reaching movements (see, e.g., Refs. [27–30]). Our model also did not include any muscle mechanics, spinal reflexes, or serial elastic elements (i.e., tendons), etc. However, increased biological noise at the *muscle* level has been shown to concurrently increase joint *torque* variability [9]. Our goal here was to elucidate the general principles by which the biomechanics of the arm and the task influence the overall choice of where to apply control (proximal versus distal). Our goal was *not* to explore any specific physiological implementation of that control. Thus, the model used here incorporated the necessary and sufficient level of complexity to address the specific control hypotheses posed.

Standard anthropometric values were obtained assuming total body mass of $M=75.0$ kg and height of $H=1.75$ m (Table 1; Ref. [31]). Inverse dynamics equations were derived from Ref. [32]. The reference joint torques (“ τ_{ref} ” in Fig. 1(b)) $[\tau_s, \tau_e]^T$ for the noise-free/control-free reaches were given by

$$\begin{bmatrix} \tau_s \\ \tau_e \end{bmatrix} = \mathbf{H}(\theta) \begin{bmatrix} \ddot{\theta}_s \\ \ddot{\theta}_e \end{bmatrix} + \mathbf{B} \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} + \mathbf{C}(\theta) \begin{bmatrix} \dot{\theta}_s \dot{\theta}_e \\ \dot{\theta}_s^2 \\ \dot{\theta}_e^2 \end{bmatrix} \quad (1)$$

where $\mathbf{H}(\theta)^{2 \times 2}$ represents the inertial matrix, $\mathbf{B}^{2 \times 2}$ denotes the torques due to damping, and $\mathbf{C}(\theta)^{2 \times 3}$ denotes the torques due to Coriolis and centrifugal forces. In this model, we assumed that there were no external forces or perturbations acting on the system. The inertia matrix $\mathbf{H}(\theta)^{2 \times 2}$ was given by

$$\mathbf{H}(\theta) = \begin{bmatrix} I_{uprox} + I_u + m_u(L_u^2 + d_f^2 + 2L_u d_f \cos(\theta_e)) & I_{fprox} + m_f(L_u d_f \cos(\theta_e)) \\ I_{fprox} + m_f(L_u d_f \cos(\theta_e)) & I_{fprox} \end{bmatrix} \quad (2)$$

Fig. 1 (a) A 2-dof torque driven arm model used to simulate three different reaching movements: anterior (ANT), left diagonal (LD), and right diagonal (RD). (b) Total ranges of motion for each joint for each reaching movement. (c) Model of the PID controller.

where L_u is the length of the upper arm and d_f denotes the distance from the elbow joint to the center of mass (COM) of the forearm. Here, m_f and m_u are the mass of the forearm and upper arm, respectively. Additionally, I_u and I_f represent the inertias of the upper arm and forearm with respect to the center of mass of the segment and $I_{uprox} = [I_u + m_u d_u^2]$ and $I_{fprox} = [I_f + m_f d_f^2]$ are the inertias of the upper arm and forearm with respect to the proximal end of the segment. The values of these parameters are given in Table 1. Here, $[\theta_s \theta_e]^T$ defines the angles of the shoulder (s) and elbow (e) joints. The torques generated by the Coriolis and centrifugal forces were given by

$$C(\theta) = \begin{bmatrix} -m_f L_u \sin(\theta_e) & 0 & -2m_f L_u d_f \theta_e \\ 0 & m_f L_u d_f \sin(\theta_e) & 0 \end{bmatrix} \quad (3)$$

The damping constants [33] were included to provide an estimate of the damping effect due to the viscoelastic structures around the joints. The damping matrix was defined as

$$B = \begin{bmatrix} 0.3 & 0.2 \\ 0.2 & 0.3 \end{bmatrix} \quad (Nms) \quad (4)$$

Table 1 Parameter values for the different arm models used in the simulations [see Eqs. (1)–(5)]. The data were obtained using Winter's measurement [31] (subscripts— u : upper arm; f : forearm). Note that all inertia (I) values are computed relative to the appropriate proximal joint. An inertia ratio (see Eq. (9)) of $IR = 1.05$ represents the typical human anthropometric mass distribution [31].

Parameter Description	Values for all IR		
Length of upper arm (L_u) (m)	0.33		
Length of forearm (L_f) (m)	0.35		
COM of upper arm (d_u) (m)	0.14		
COM of forearm (d_f) (m)	0.018		
Segment masses and inertias	IR = 0.25	IR = 1.05	IR = 4.00
Mass of upper arm (m_u) (kg)	0.915	2.100	2.9905
Mass of forearm (m_f) (kg)	2.610	1.425	0.5345
Inertia of upper arm (I_u) ($kg \cdot m^2$)	0.0291	0.0668	0.0951
Inertia of forearm (I_f) ($kg \cdot m^2$)	0.1161	0.0634	0.0238

Equation (1) was used to formulate the differential equations to calculate the forward kinematics

$$\begin{bmatrix} \ddot{\theta}_s \\ \ddot{\theta}_e \end{bmatrix} = H^{-1}(\theta) \left(\begin{bmatrix} \tau_s \\ \tau_e \end{bmatrix} - B \begin{bmatrix} \dot{\theta}_s \\ \dot{\theta}_e \end{bmatrix} - C(\theta) \begin{bmatrix} \dot{\theta}_s \dot{\theta}_e \\ \dot{\theta}_s^2 \\ \dot{\theta}_e^2 \end{bmatrix} \right) \quad (5)$$

The differential equations were solved by using numerical integration with trapezoidal rule (step size = 0.002). A simple numerical integration code was implemented in MATLAB® (The Math Works Inc, Natick, MA) to solve the differential equation. Although MATLAB® offers numerous alternatives to solving the differential equations, our code yielded similar results at a smaller computational cost.

This model was used to simulate reaching movements in three distinct directions: anterior (ANT), left diagonal (LD), and right diagonal (RD) (see Fig. 1(a)). These directions were chosen to test a wide range of motion of the shoulder and elbow joints (Fig. 1(b)). For the right arm, a LD reach required a larger range of movement at shoulder, but less at the elbow, while a RD reach required a larger range of movement at the elbow, but less at the shoulder. Simulating these three directions allowed us to further highlight the differences of proximal versus distal control in the presence of noise and biomechanical variation. Furthermore, these directional tasks provided a broader scope within which to capture the diversity of underlying control mechanisms across different reaching tasks [34–36]. This allowed us to explicitly explore how the nervous system could exploit redundancy in the choice of where to apply *feedback control* (i.e., at the proximal versus distal joint versus both joints) to maximize task performance, even in a task that exhibited no kinematic redundancy.

2.2 Nominal Reaching Movement. The distance from each starting point to each target was set at 50 cm to yield slightly less than fully extended reaching movements in all reaching directions for a model with a total arm length of 68 cm (Table 1). For anterior movements, the starting pose of the arm was set at 10 cm anterior to the shoulder joint (Fig. 1(a)). For diagonally directed movements, the starting positions were offset at 45 deg in the corresponding direction (Fig. 1(a)). The movement time was set at

1 s. Within each trial, the nominal movement was defined by a feed-forward minimum jerk trajectory [37,38]. Minimum jerk is just one of many computational models that accurately predict average trajectories of the hand during reaching [39–42]. For straight-line reaching movements, this model accurately predicts the basic kinematic features exhibited by humans during reaching. The minimum jerk theory states that humans tend to minimize the net jerk (i.e., the derivative of acceleration) of the hand during the reaching movement. The cost function to be minimized is thus

$$C = \frac{1}{2} \int_0^{t_f} \left(\left(\frac{d^3x}{dt^3} \right)^2 + \left(\frac{d^3y}{dt^3} \right)^2 \right) dt \quad (6)$$

where (x, y) denotes the Cartesian coordinates of the hand and $t_f = 1$ s is the total duration of the reaching movement. Assuming that motion starts and ends with zero velocity and zero acceleration and that (x_0, y_0) , and (x_f, y_f) denote the initial and final positions of the hand, respectively, the solution of Eq. (5) yields a trajectory of the hand that is described in the Cartesian plane as a 5th order polynomial

$$\begin{aligned} x(t) &= x_0(x_0 - x_f)(-6\zeta^5 + 15\zeta^4 - 10\zeta^3) \\ y(t) &= y_0(y_0 - y_f)(-6\zeta^5 + 15\zeta^4 - 10\zeta^3) \end{aligned} \quad (7)$$

where $\zeta = t/t_f$. Once this nominal hand trajectory was specified, joint kinematics were calculated using inverse kinematics. Nominal joint torques required to achieve this trajectory were then calculated using inverse dynamics (see Eq. (1)). Because the task was restricted to the 2D plane, there was a one-to-one mapping of the endpoint (i.e., hand) motion to these joint torque profiles. Here we considered only reaching movements directed away from the body. Movements directed towards the body would have yielded the same kinematics and inverse dynamics (see Fig. 2), except in reverse time.

2.3 Signal-Dependent Noise. Motor noise was added to the feed-forward profiles of the elbow and shoulder joint torques (see Fig. 2) to determine the relative sensitivity of the system to distal and/or proximal noise. This noise was specified to be signal-dependent [3,4], such that the noise amplitude increased proportionally with an increase in muscular activity (see Fig. 2). Osu [9] demonstrated that increases in *muscle* (i.e., electromyogram) variability resulted in increased joint torque variability. Therefore, while *neuromuscular noise* initially arises from muscle forces and/or activations, the inherent signal-dependent noise [3,4] generated during muscle activation is also reflected in the resulting joint torques [9]. We, therefore, assumed the noise added to these net joint torques reasonably reflected the net effect of the neuromuscular noise in the system. In the model, this noise was added either to the elbow torque only, to the shoulder torque only, or simultaneously to both the elbow and shoulder torques (see Fig. 2).

The applied signal-dependent-noise $\mathbf{N}_i$ was randomly distributed and scaled to be proportional to the torque output (τ) at each joint (see Fig. 2(b))

$$\mathbf{N}_i = \begin{bmatrix} N_{s,i} \\ N_{e,i} \end{bmatrix} = 0.3 \begin{bmatrix} \tau_{s,i} \cdot \eta_{s,i} \\ \tau_{e,i} \cdot \eta_{e,i} \end{bmatrix} \quad (8)$$

where i denotes the individual time step within the reaching movement and the $\eta_{s,i}$ terms were random values chosen from a uniform distribution on the interval $[-1, +1]$ generated using the MATLAB® “rand” function. Typical profiles of the noise at the shoulder and elbow joint are shown in Fig. 2(b). This noise was then added to the nominal torque required to make each reaching movement.

2.4 Control Model. While motor noise is ubiquitous in movement [1], humans do use sensory feedback to help mitigate

Fig. 2 (a) Nominal torque profiles for the shoulder and elbow joint during anterior reaching without the influence of noise. (b) Shoulder joint signal-dependent noise profile. (c) Elbow joint signal-dependent noise profile.

its effects on task performance. Therefore, within each trial, standard proportional-integrative-derivative (PID) controllers (see Fig. 1(c)) were implemented to simulate within-trial torque adjustment. The same PID controller was used to control the elbow and shoulder joint torques, either independently or jointly. Similar types of controllers [43,44] have been shown to adequately capture the dynamics of relatively typical reaching movements. These controllers adjusted the performance of the system proportionally to the torque error output and its derivative. This control law was given by

$$\mathbf{V}(t) = \mathbf{k}_p \cdot \mathbf{e}(t) + \mathbf{k}_i \cdot \int \mathbf{e}(t) dt + \mathbf{k}_d \cdot \frac{d}{dt} \mathbf{e}(t) \quad (9)$$

where $\mathbf{e}(t)$ was the relevant torque error (i.e., elbow or shoulder) and $\mathbf{V}(t)$ was the feedback control effort required to correct for deviations in the torque due to motor noise at the relevant joint(s). Given the one-to-one mapping between hand kinematics and joint torques, correcting these torque errors was equivalent to correcting endpoint errors. Control was only applied when noise was present at both the elbow and shoulder joint. To apply control at the elbow only, we took $\mathbf{e}(t) = [0 \ e_e(t)]^T$ and $\mathbf{V}(t) = [0 \ V_e(t)]^T$. To apply control at the shoulder only, we took $\mathbf{e}(t) = [e_s(t) \ 0]^T$ and $\mathbf{V}(t) = [V_s(t) \ 0]^T$. To simultaneously apply control at both the elbow and shoulder, we took $\mathbf{e}(t) = [e_s(t) \ e_e(t)]^T$ and $\mathbf{V}(t) = [V_s(t) \ V_e(t)]^T$. For all three controllers, the control constants were diagonal matrices

$$\mathbf{k}_p = \begin{bmatrix} k_p & 0 \\ 0 & k_p \end{bmatrix}, \quad \mathbf{k}_i = \begin{bmatrix} k_i & 0 \\ 0 & k_i \end{bmatrix}, \quad \mathbf{k}_d = \begin{bmatrix} k_d & 0 \\ 0 & k_d \end{bmatrix} \quad (10)$$

where $k_p = 0.3$, $k_i = 0.2$, and $k_d = 0.1$ were the controller gains. These proportionality constants were determined using the Ziegler-Nichol rule [45], which heuristically tuned the controller to find constants that satisfied specified performance requirements.

Fig. 3 The biomechanical properties of the arm were manipulated by varying the inertia distribution along the arm

The same control values were used for all simulations for all conditions to ensure that the results did not depend on the optimization of these parameters. The controller iteratively minimized the noise at every time step during each movement until the noise was eliminated within a specified tolerance. Although more sophisticated control schemes certainly do exist that are more physiologically “realistic” (indeed, real biological controllers are far less effective than the controllers used here), the critical aspect to *this* study is that we applied the *same* type of control to both joints in the same way.

2.5 Simulations and Analyses

2.5.1 Simulations. Two different sets of conditions were simulated to determine how noise and control affected the endpoint error and net work during planar reaching. The first set of simulations compared the effect of noise at the elbow versus noise at the shoulder on the endpoint error and net work in the absence of any control at the joints. The second set of simulations compared how, when noise was present at both joints, applying distal and/or proximal control affected the endpoint error and net work.

To investigate the effects of inertial distribution in the upper extremity, we manipulated the masses of the upper arm and forearm to generate different inertia ratios (see Fig. 3), while keeping the total mass and total length of the arm constant. The total mass of the arm was kept constant to prevent introducing additional loads into the system. The inertia ratio (IR) was defined as

$$IR = \frac{I_u}{I_f} \equiv \frac{\text{Inertia of upper arm}}{\text{Inertia of forearm}} \quad (11)$$

where I_u and I_f define the inertia of the upper arm (u) and forearm (f) with respect to the center of mass of each segment. Three inertia ratios were tested (see Fig. 3). The anthropometric arm, based on standard human data, had an $IR \approx 1.05$ (Table 1). The other two ratios ($IR = 0.25$ and $IR = 4.0$) were chosen to represent dramatic shifts of the inertia in both directions. While these two alternative IRs do not represent biologically realistic systems, the results from these simulations allowed us to explicitly determine how the biomechanical properties of the human arm might influence the choice of any control strategy the nervous system might choose to use to minimize noise.

Simulations were implemented in MATLAB® (The Math Works Inc, Natick, MA). Each condition was simulated for 30 trials and the average values were recorded.

2.5.2 Dependent Measures. The endpoint error is a direct measure of the success in the task. Endpoint errors in position were calculated as the absolute deviation from the desired endpoint location (x_d, y_d), as specified by the nominal feed-forward minimum jerk trajectory (Eq. (7)). This error was defined as

$$Err_j = \sqrt{(x_j - x_d)^2 + (y_j - y_d)^2} \quad (12)$$

where (x_j, y_j) denoted the endpoint location at the completion of each trial j . The minimum jerk reaching trajectories used here imposed zero velocity and zero acceleration at the beginning and end of each reaching movement, which also yielded zero torque (see Fig. 2(a)). Since the noise applied was proportional to these torques (see Fig. 2(b)), we assumed that any errors in torque, velocity, or acceleration would be quite small compared to the position errors.

Total net work (TNW) is a direct measure of the work required to complete the task. This assumes that people try to complete the task as accurately as possible with as little effort as necessary. Alexander [39] demonstrated that *one* possible strategy that drives human arm trajectories is to minimize the energy cost [46,47]. Therefore, it is possible that the distal-proximal control strategy could yield more energetically efficient movements. Here, energetic cost was only used as performance metric and not as an optimization parameter for the system. The TNW was calculated as the total net work (in joules) required to drive the system to the reference state under the presence of noise. The reference state was fully specified by the minimum jerk motion. The TNW included the feedback (PID controller), feed-forward (minimum jerk), and noise components of the effort required to execute each movement. The TNW for each trial was thus calculated by numerically integrating the absolute value of the power curve

$$TNW_j = \sum_{i=1}^k |\tau_{t(i)} \cdot \dot{\theta}_{t(i)}| \Delta t \quad (13)$$

where k denotes the number of discrete time steps within each trial ($k = 500$) and $\tau_{t(i)}$ denotes the total *output* torque (“ τ_{out} ” in Fig. 1(b)) at each joint, including the torque due to noise and feedback controller.

2.5.3 Statistical Analyses. Endpoint error (Err) and total net work (TNW) were analyzed for both sets of simulations. To analyze the effects of adding *noise* (in the absence of control) on the endpoint error and net work, 3-factor analysis of variance (ANOVAs) were used to determine both the main effects and interaction effects across noise locations (distal or proximal), directions (ANT, LD, RD), and the 3 inertia ratios. Estimated marginal means tests were used to make individual post hoc comparisons across the different levels of each factor. Within each direction, 2-factor ANOVAs were used to identify significant effects of noise and inertia ratio on endpoint error and net work.

To analyze the effects of applying *control* (in the presence of noise) on the endpoint error and net work, 3-factor ANOVAs were used to determine both the main effects and interaction effects across the joint control schemes (no control, shoulder control only, elbow control only, elbow + shoulder control), directions (ANT, LD, RD), and the 3 inertia ratios. Estimated marginal means tests were used to make individual post hoc comparisons across the different levels of each factor. Within each direction, 2-factor ANOVAs were used to identify the significant effects of the control and inertia ratio on the endpoint error and net work.

Fig. 4 Endpoint errors for reaching movements in the (a) anterior direction, (b) left diagonal direction, and (c) right diagonal direction when noise was independently applied at the elbow and shoulder joint. Error bars indicate $\pm$ standard deviations.

3 Results

3.1 Distal Versus Proximal Noise

3.1.1 Endpoint Error. In the absence of any control at the joints, there were significant differences in the endpoint error (Err) across all reaching directions ($p < 0.05$), inertia ratios ($p < 0.05$), and noise locations ($p < 0.05$) (see Fig. 4), when noise was independently applied either at the proximal (shoulder) joint or distal (elbow) joint. For movements in the anterior (ANT) direction, noise applied at the elbow resulted in significantly larger endpoint errors (Err = 5.77 cm) than noise applied at the shoulder (Err = 1.48 cm, $p < 0.05$). The same trend was observed across all inertia ratios for movements in the ANT direction. As more mass was shifted toward the upper arm, creating a larger inertia ratio, there were significant increases in endpoint error due to noise at distal joint (from 2.89 cm to 9.53 cm, $p < 0.05$), but not due to noise at the proximal joint.

Similar trends were also observed for movements in the left diagonal (LD) direction (see Fig. 4(b)). Noise applied at the distal joint had a significantly larger effect on the endpoint error (Err = 6.107 cm) than noise applied at the proximal joint (Err = 2.52 cm, $p < 0.05$). This was true across all inertia ratios. Similarly, as the inertia ratio increased, the endpoint error due to distal noise also increased (from Err = 4.13 cm to Err = 8.4 cm, $p < 0.05$). In contrast to the ANT, proximal noise also generated more endpoint error (from Err = 1.6 cm to Err = 3.64 cm, $p < 0.05$) with increases in the inertia ratio.

For movements in the right diagonal (RD) direction (Fig. 4(c)), noise at the distal joint also generated greater endpoint error (Err = 4.63 cm) than noise applied at the proximal joint (Err = 3.63 cm, $p < 0.05$). Similar to the LD direction, higher iner-

tia ratios also yielded a greater endpoint error when noise was applied at the distal joint (from Err = 2.7 cm to Err = 7.2 cm, $p < 0.05$) and the proximal joint distal (from Err = 3.2 cm to Err = 4.2 cm, $p < 0.05$). The lowest inertia ratio in the RD direction generated the only instance where the proximal noise (Err = 3.2 cm) generated more endpoint error than the distal noise (Err = 2.27 cm, $p < 0.05$).

3.1.2 Net Work. Similar to the endpoint error, there were significant differences in the net work across different reaching directions ($p < 0.05$), inertia ratios ($p < 0.05$), and noise locations ($p < 0.05$) (see Fig. 5). In general, the average net work in the LD direction (see Fig. 5(b)) (TNW = 3.94 J) was significantly larger than the average net work in the ANT direction (see Fig. 5(a)) (TNW = 1.83 J, $p < 0.05$) and the RD direction (see Fig. 5(c)) (TNW = 1.89 J, $p < 0.05$). In addition, the between-trial variances on the energetic cost were significantly smaller than the between-trial variances for endpoint error due to distal and proximal noise. Thus, the TNW was less sensitive to changes in noise than the endpoint errors (Err).

In the ANT direction (see Fig. 5(a)), the net work was more affected by distal noise (TNW = 1.98 J) than by proximal noise (TNW = 1.68 J, $p < 0.05$). However, their mean difference was small ($\Delta = 0.293$ J). As the inertia ratio increased, the effect of the distal noise (TNW = 2.53 J to TNW = 1.67 J, $p < 0.05$) and the proximal noise (TNW = 2.39 J to TNW = 1.11 J, $p < 0.05$) on the net work decreased. This is true across all three directions. However, in the LD direction, the opposite trends were observed (see Fig. 5(b)) when applying distal and proximal noise. Noise applied at the proximal joint (TNW = 4.23 J) generated more energetic cost than noise applied at the distal joint (TNW = 3.65 J,

Fig. 5 Total net work for reaching movements in the (a) anterior direction, (b) left diagonal, and (c) right diagonal when noise was independently applied at the elbow and shoulder joint. Error bars indicate $\pm$ standard deviations.

Fig. 6 Endpoint errors due to the change in the control scheme for reaching movements in the (a) anterior direction, (b) left diagonal, and (c) right diagonal when noise was present at both joints. Error bars indicate $\pm$ standard deviations.

$p < 0.05$). The RD direction (see Fig. 5(c)) exhibited similar trends to the ANT (Fig. 5(a)). The net work, on average, was significantly larger when noise was applied at the distal joint (TNW = 2.0 J) than when noise was applied at the proximal joint (TNW = 1.76 J, $p < 0.05$)

3.2 Distal Control Versus Proximal Control

3.2.1 Endpoint Error. When noise was present at both the shoulder and elbow joint simultaneously, there were significant differences in the endpoint error across all directions ($p < 0.05$), inertia ratios ($p < 0.05$), and control locations ($p < 0.05$) (see Fig. 6).

In the ANT (see Fig. 6(a)), applying control at the proximal joint (Err = 5.08 cm) generally *increased* endpoint error, compared to the no control condition (Err = 4.12 cm, $p < 0.05$). However, applying control at either the distal joint (Err = 1.75 cm) or both joints (Err = 0.714 cm) significantly *reduced* endpoint error when compared to the no control condition ($p < 0.05$). Generally, applying control at both joints simultaneously improved task performance over conditions where only the distal joint was controlled. There were also significantly larger increases in endpoint error for the no control condition (from 1.36 to 8.4 cm, $p < 0.05$) and the proximal joint control condition (2.29 to 9.17 cm, $p < 0.05$) when more mass was shifted to the upper arm. Yet, the increases in inertia ratio did not affect the endpoint error generated by elbow control or the shoulder + elbow control condition.

This trend was also observed in the LD and RD direction. In the LD direction (see Fig. 6(b)), there were significant differences between the no control condition (Err = 5.92 cm) and the shoulder control condition (Err = 5.85 cm) ($p < 0.05$) across all inertia ratios. However, the mean difference was small ($\Delta = 0.07$ cm).

Applying elbow control (Err = 2.81 cm) and shoulder + elbow control (Err = 0.63 cm) greatly reduced the endpoint error when compared to the no control ($p < 0.05$) and shoulder control conditions ($p < 0.05$). For movements in the RD direction (see Fig. 6(c)), all combinations of joint control significantly reduced the endpoint errors from the no control condition ($p < 0.05$). Applying shoulder control reduced the endpoint error from Err = 6.7 cm to Err = 4.5 cm ($p < 0.05$) while applying elbow control reduced the endpoint error to Err = 3.82 cm ($p < 0.05$). Furthermore, when both joints were simultaneously controlled, the endpoint error was reduced to Err = 0.73 cm ($p < 0.05$).

3.2.2 Total Net Work. When noise was present at both the shoulder and elbow joint simultaneously, there were significant differences in the net work across all different directions ($p < 0.05$), inertia ratios ($p < 0.05$), and control locations ($p < 0.05$) (see Fig. 7).

For movements in the ANT (see Fig. 7(a)), applying control at either the shoulder, elbow, or both joints reduced the net work compared to the no control condition. While shoulder control was statistically significant when compared to the no control condition, their mean differences were very small ($\Delta = 0.03$ J). Applying control at the elbow significantly reduced the net work (TNW = 1.77 J) compared to the no control condition (TNW = 2.07 J) ($p < 0.05$). Similarly, applying control at both joints reduced net work to TNW = 1.73 J ($p < 0.05$). As the inertia ratio increased, there were significant decreases in net work across all control schemes. The net work decreased from TNW = 2.60 J to TNW = 1.77 J ($p < 0.05$) for the no control condition and from TNW = 2.55 J to TNW = 1.72 J ($p < 0.05$) for the shoulder control condition as the inertia ratio increased. Similarly, as the inertia ratio increased, net work decreased from TNW = 2.43 J to

Fig. 7 Total net work due to the change in the control scheme for reaching movements in the (a) anterior direction, (b) left diagonal, and (c) right diagonal when noise was present at both joints. Error bars indicate $\pm$ standard deviations.

TNW = 1.24 J ($p < 0.05$) during the elbow control condition and from TNW = 2.39 J to TNW = 1.2 J ($p < 0.05$) when control was applied at both joints.

For movements in the LD direction (see Fig. 7(b)), applying shoulder control (TNW = 3.71 J) required a significantly less energetic cost than all other conditions ($p < 0.05$). Using only elbow control (TNW = 4.25 J) generated the most energetic cost, even when compared to the no control condition (TNW = 4.1 J) ($p < 0.05$). This trend was different than the anterior or RD directions. When control was applied at both joints, the energetic cost (TNW = 3.8 J) was significantly less than applying elbow control ($p < 0.05$), but greater than shoulder control ($p < 0.05$). However, the mean difference was very small ($\Delta = 0.69$ J). As the inertia ratio increased, there were significant decreases in the energetic cost across all control conditions. The no control and shoulder control conditions reduced the energetic cost by 2.32 J ($p < 0.05$) as the inertia ratio increased. Similarly, as the inertia ratio was increased, net work decreased by 3.2 J ($p < 0.05$) during elbow only control and by 1.11 J ($p < 0.05$) when control was applied at both joints.

Movements in the RD direction (see Fig. 7(c)) exhibited similar trends to the ANT (see Fig. 7(a)). The no control condition generated the greatest energetic cost (TNW = 2.11 J), while controlling both joints required the least energetic cost (TNW = 1.69 J). While there were statistically significant differences between the shoulder control and no control conditions ($p < 0.05$), the mean value difference was small ($\Delta = 0.07$ J). Controlling either the elbow only (TNW = 1.78 J) or both joints significantly decreased the energetic cost from the no control condition ($p < 0.05$). Furthermore, while there were statistically significant differences between these two conditions, the mean difference was, again, small ($\Delta = 0.09$ J). Similar to the ANT movements, as the inertia ratio increased, the net work decreased across all control conditions. During the no control condition, the energetic cost reduced by 0.7 J ($p < 0.05$), while during shoulder control the energetic cost decreased by 0.55 J ($p < 0.05$) as the inertia ratio increased. Similarly, as the inertia ratio increased, the net work decreased by 0.84 J ($p < 0.05$) during the elbow control condition and by 0.55 J ($p < 0.05$) when control was applied at both joints.

4 Discussion

Determining how the nervous system deals with inherent redundancy is one of the central questions of motor control research [19,20,42]. Likewise, one of the most fundamental issues the nervous system has to deal with in solving this problem is the ubiquitous noise that is inherent in biological systems [1–3]. Here, we studied a planar reaching task that did not exhibit kinematic redundancy, but *was* redundant in the sense that any controller trying to regulate the movements of that arm has to decide whether to apply more or less effort to reduce the influence of noise emanating from either the proximal (shoulder) joint, or the distal (elbow) joint, or both joints equally. We specifically determined how the biomechanical factors of the arm (inertia ratio) and the task (reaching direction) influenced how different combinations of motor noise and/or control applied at each joint torque in turn affected reaching accuracy and total net work.

In general, for all three reaching directions and all three inertia ratios (IR) tested, adding noise to the elbow (distal) joint always incurred significantly greater endpoint errors than imposing noise at the shoulder (proximal) joint (see Figs. 4(a)–4(c)) with only one exception at the lower inertia for movements in the RD direction (see Fig. 4(c)). Conversely, the total net work required to eliminate the effects of this noise was either not different, or slightly greater, when the noise was applied to the shoulder (proximal) joint than to the elbow (distal) joint (see Figs. 5(a)–5(c)). These results largely confirmed previous experimental observations [14,48]. While the movements in the ANT and RD directions showed that shoulder control had a slightly lower energetic cost than elbow control, the differences were very small. The small increases in energetic cost were greatly outweighed by the significant

decreases in endpoint error. Since the *only* difference between these conditions in our simulations was where this noise was applied, these results confirm that the noise applied at the shoulder was dampened by the larger inertial load of the upper arm plus forearm, whereas the noise applied at the elbow was transmitted mostly unimpeded to the endpoint.

Likewise, when noise was simultaneously imposed at both joints, applying distal control was always more effective than applying proximal control for improving endpoint accuracy (see Figs. 6(a)–6(c)) with only one exception at the lower inertia ratio for movements in the RD direction (see Fig. 6(c)). However, the magnitudes of these reductions varied for the three different movement directions. Additionally, using distal control generally required less total net work than proximal control (see Figs. 6(a) and 6(c)). However, during the LD movements, more net work was required during distal control than proximal control. For the LD movements, the task required greater shoulder motion (see Fig. 1(b)); therefore, it is possible that controlling the elbow would require larger net work. However, the small increase in energetic cost was compensated by the larger reduction in endpoint error (see Fig. 6(b)). These results suggest that applying distal control is the most energetically efficient strategy to maximize task performance. Together, these results strongly confirm both of our first two hypotheses, namely, that (1) reaching performance in all cases was far more sensitive to distal (elbow) noise than to proximal (shoulder) noise, and that (2) applying only distal (elbow) control was far more effective than applying only proximal (shoulder) control.

The results also showed the significant effects of biomechanics on task performance. As the inertia distribution was shifted to the upper arm (IR = 4.0), endpoint errors increased. When noise was applied at the distal joint, at a smaller IR, the inertia was concentrated at the distal joint, thus, the forearm provided a natural biological damper to the noise in the system. As the inertia distribution was shifted to the upper arm, the inertia load at the upper arm essentially had no effect on the noise at the distal joint independent of the direction of the task. The inertia effects were also evident in the net work. When the forearm was large (IR = 0.25), more *net* work was required to both move and control the mass of the distal segment. As the mass was shifted to the upper arm, less total net work was required. These results were consistent across all reaching directions, noise conditions, and control conditions (see Fig. 7). These results also explained why less net work was expended for movements in the RD direction than in the LD direction. For the RD movements, which required more elbow extension, the noise and net work depended mainly on the distal joint. For the LD movements, where the noise was mainly driven by the shoulder torque, more net work was expended to move and control the arm.

Somewhat counter-intuitively, for most reaching directions and inertia ratios, the total net work required to both move *and* control the system tended to decrease as control was applied at more joints (see Fig. 7). In general, applying additional control to reduce noise will increase energy expenditure. However, Fig. 7 shows that controlling both joints simultaneously can be more efficient overall, because it allows the system to exploit the natural mechanical coupling between the two joints. This natural passive mechanical coupling helps cancel the effects of the noise across both joints more rapidly, thus reducing the total net work required to both move and control the system.

Endpoint accuracy was significantly different, depending on the direction of the reaching task (see Fig. 4). When movements relied heavily on elbow extension (RD; see Fig. 4(c)); noise at the shoulder joint had far greater effects on endpoint performance when compared to the shoulder intensive (LD; see Fig. 4(b)) or balanced (ANT; see Fig. 4(a)) directions. Again, when the source of the noise depended on the torque of the distal joint, this had the most significant effect on the endpoint error. Therefore, controlling that noise naturally reduced the endpoint error with less net work. Similar trends were also exhibited for the net work across

all three reaching directions (see Fig. 5). The net work required in the RD direction was significantly less than in the LD direction. These results emphasize the critical function of distal noise and control during reaching movements. Within each inertia ratio for all noise conditions, there were significant decreases in net work as more inertia was shifted to the upper arm (i.e., $IR = 4.0$). Generally, a relatively larger forearm required more net work for all conditions, except for movements in the LD direction, where the task is more shoulder intensive. Together, these results also confirm our third hypothesis, namely, that (3) the effects of noise and control are strongly influenced by biomechanical factors (i.e., reaching direction and/or inertial properties).

Noise is always present in the human neuro-musculo-skeletal system [1–3]. During movement, this noise is selectively suppressed or ignored by the nervous system. Determining how the nervous system compensates for this noise is vital to understanding movement coordination [19,24,42]. Experimental paradigms lack the ability to unequivocally determine how, or if, the nervous system uses distal-proximal control strategies to compensate for motor noise and generate desired movements. The present study provides a rigorous computational analysis which clearly demonstrates that biomechanical factors related to both the system configuration (e.g., arm inertial properties) and the task being performed (e.g., reaching directions) play a defining role in determining how the nervous system should most effectively apply the control effort across the shoulder and elbow joints in order to maximize system performance, while also limiting the expended energy cost. These insights help reveal a more comprehensive picture of why the nervous system chooses to control certain parameters more than others during these types of tasks.

The simplified model used here does not fully represent all of the intrinsic complexities of the biological system at the muscle or neural level, nor does it capture the abundance of redundancy in the motor system. Individual muscles can transmit or absorb power from limb segments not directly connected to those muscles [49]. Likewise, agonist and antagonist muscle groups likely play different roles during dynamic and isometric tasks [50–54]. These interactions could significantly affect how the nervous system controls movements. However, implementing a more complicated muscle-driven model would have introduced additional layers of redundancy (i.e., now at the muscle level and at the joint level). This would have, in turn, made it far more difficult to precisely determine which differences we observed might be due to redundancy at the joint level versus the muscle level. Thus, the torque-driven model implemented here did provide an appropriate tool to examine, at the macroscopic level, how even the simplest redundancy can significantly affect task performance.

Biomechanically, there are advantages in applying distal control over proximal control. The location of the noise and the inertia distribution of the arm affect the performance of the task as well as the total control effort required to minimize the noise in the system. These results could potentially explain how humans learn or adapt to different tasks based on the sequential control of proximal-to-distal joints [13,15]. Humans could potentially initially acclimate to the task using proximal control and then later refine their movements using more effective distal control, similar to the hypothesis posed in Ref. [12]. Furthermore, humans could exploit the greater sensitivity of the distal joint to noise to generate more accurate movements using minimal energy. Our results demonstrate that the human nervous system potentially takes advantage of these control strategies to minimize the effects of noise within the neuromuscular system during movement.

Our simulations provide a well-grounded theoretical framework from which to interpret previous experimental results [12–15], which suggest that humans appear to prefer to impose greater control over distal joints than over proximal joints, but do not explain *why*. Our results provide the first analytical evidence to concretely determine why this is: because it is both more effective and less costly. Although it has often been hypothesized that human generate arm trajectories that minimize muscle energy, a number of

studies have questioned this assumption (e.g., Refs. [35,55]) and there remains much debate about exactly what is being *optimized* during arm movement [41]. Here, our model made no explicit attempts to optimize energy expenditure. Instead, we used the energy cost merely as an output metric to quantify performance. Our results demonstrate that applying the appropriate control (i.e., distal versus proximal) in the presence of noise could lead to lower energy consumption. Thus, our findings support the idea that people adopt control strategies based, at least partly, on the “minimum intervention principle” [17,19,20,24,25]. That is, they expend far less effort to minimize fluctuations at the proximal joints because those fluctuations have only minimal effects on the final task performance.

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