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Title: The energetic basis for smooth human arm movements
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Abstract

The central nervous system plans human reaching movements with stereotypically smooth kinematic trajectories and fairly consistent durations. Smoothness seems to be explained by accuracy as a primary movement objective, whereas duration seems to avoid excess energy expenditure. But energy does not explain smoothness, so that two aspects of the same movement are governed by seemingly incompatible objectives. Here we show that smoothness is actually economical, because humans expend more metabolic energy for jerkier motions. The proposed mechanism is an underappreciated cost proportional to the rate of muscle force production, for calcium transport to activate muscle. We experimentally tested that energy cost in humans (N=10) performing bimanual reaches cyclically. The empirical cost was then demonstrated to predict smooth, discrete reaches, previously attributed to accuracy alone. A mechanistic, physiologically measurable, energy cost may therefore unify smoothness and duration, and help resolve motor redundancy in reaching movements.

Introduction

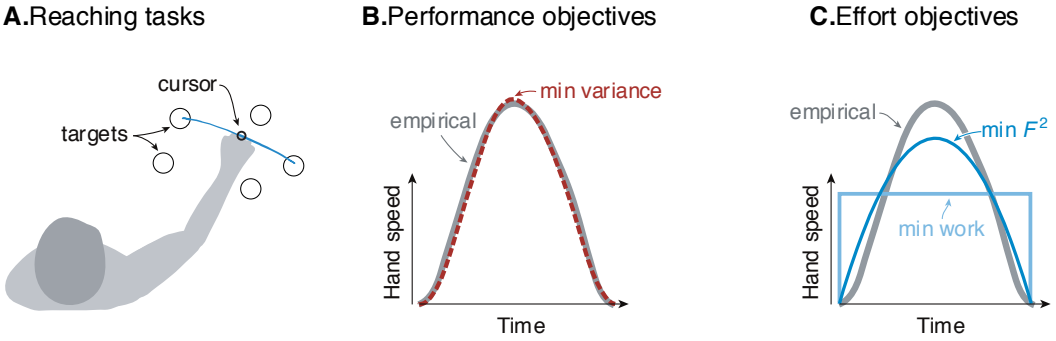

Figure 1. Goal-directed reaching tasks and optimization criteria. (A.) Typical experiments for point-to-point movements between targets. (B.) Hand speed trajectories vs. time. Kinematic objectives such as minimizing jerk or variance predict the observed smooth, bell-shaped profiles for hand speed. (C.) Effort-based objectives such as minimizing work or squared muscle force or activation predict trajectories that are not smooth, or not bell-shaped (Nelson 1983).

Upper extremity reaching movements are characterized by a stereotypical, bell-shaped speed profile for the hand's motion to its target (Fig. 1A). The profile's smoothness seems to preserve kinematic accuracy (Harris and Wolpert 1998), and have little to do with the effort needed to produce the motion. But effort or energy expenditure appear to affect other aspects of

reaching (Huang et al. 2012; Shadmehr et al. 2019), and influence a vast array of other animal behaviors and actions (Alexander 1996). It seems possible that effort or energy do influence the bell-shaped profile, but have gone unrecognized because of incomplete quantification of such costs. If so, then dynamic goals including effort could play a key role in movement planning.

The kinematic goal for accuracy may be expressed quantitatively as minimization of the final endpoint position variance (Harris and Wolpert 1998). Non-smooth motions introduce inaccuracy because motor noise increases with motor command amplitude, a phenomenon termed signal-dependent noise (Matthews 1996; Sutton and Sykes 1967) . It predicts well the speed profiles for not only the hand but also the eye. It explains why more curved or more accurate motions need to be slower, and also subsumes an older theory for minimizing kinematic jerk (Flash and Hogan 1985). The single objective of movement variance explains multiple aspects of smooth movements, and makes better predictions than competing theories (Diedrichsen et al. 2010; Haith et al. 2012; Todorov 2004).

There are nonetheless reasons to consider effort. Many optimal control tasks must include an explicit objective for effort, without which movements would be expected to occur at maximal effort ("bang-bang control," Harris and Wolpert 1998; Bryson and Ho 1975). In addition, metabolic energy expenditure is substantial during novel reaching tasks, and decreases as adaptation progresses (Huang et al. 2012). Such a cost also helps to determine movement duration and vigor (Shadmehr et al. 2016), not addressed by the minimum-variance hypothesis. Indeed, optimal control studies have long examined effort costs such as for muscle force (Kolossiatis et al. 2016), mechanical work (Alexander 1997), squared force or activation (Nelson 1983; Ma et al. 1994), or "torque-change" (integral of squared joint torque derivatives; Uno et al. 1989). But such costs produce non-smooth velocity profiles (Fig. 1B), or lack physiological justification, or both. Some studies have included explicit models of muscle energy expenditure, but without testing such costs physiologically (Kistemaker et al. 2010). There is good evidence that energy expenditure is relevant to reaching (Shadmehr et al. 2016), but no physiologically tested cost function predicts the velocity profiles of reaching as well as the minimum variance hypothesis.

The issue could be that metabolic energy expenditure for muscle is not quantitatively well-understood. Energy is expended in proportion to force and time ("tension-time integral") in isometric conditions (Crow and Kushmerick 1982), and in proportion to mechanical work in steady work conditions (Barclay 2015; Margaria 1976), neither of which apply well to reaching. There is, however, a less-appreciated cost for muscles that increases with brief bursts of intermittent or cyclic action. It is due to active calcium transport to activate/deactivate muscle , observed in both isolated muscle preparations (Hogan et al. 1998) and whole organisms (Bergstrom and Hultman 1988). It has also been hypothesized quantitatively (Doke and Kuo 2007), as a cost per contraction roughly proportional to the rate of change of muscle force. Such a cost has indeed been observed in a variety of lower extremity tasks (Dean and Kuo 2011; Doke et al. 2005; van der Zee and Kuo 2020). It has a mechanistic and physiological basis, is supported by experimental evidence, and would appear to penalize jerky motions due to their energetic cost. What is not known is whether this energetic cost can explain reaching.

We therefore tested whether there is an energetic basis for reaching movements. We did so by measuring oxygen consumption during steady-state cyclic reaching motions. The expectation was that the proposed force-rate cost would cost metabolic energy in excess of what could be explained by mechanical work. We next applied the empirically derived cost for both force-rate and work to an optimal control model of discrete, point-to-point reaching, and tested whether it could predict the smooth, bell-shaped velocities normally attributed to minimum-variance. If the proposed cost is observed as expected and predicts bell-shaped profiles, it could potentially provide a re-interpretation of existing theories based on kinematics alone, and integrate energy expenditure into a general framework for planning reaching movements.

Materials and Methods

There were three main components to this study: (1) a simple cost model, (2) a set of human subjects experiments with cyclic reaching, and (3) an application of the model to predict discrete reaching trajectories. The model predicts that metabolic cost should increase with the hypothesized force-rate measure, particularly for faster frequencies of movement. Key to the experiment (Fig. 2) was to isolate the hypothesized force-rate cost, by applying combinations of movement amplitude and frequency that control for the cost of mechanical work. This primary test was accompanied by a secondary, cross-validation test, with different combinations of movement amplitude and frequency. Finally, we applied this same force-rate cost to the prediction of discrete reaching movement trajectories. This was to test whether the energetic cost, derived from continuous, cyclic reaching movements, could also predict the smooth, discrete motions often found in the literature.

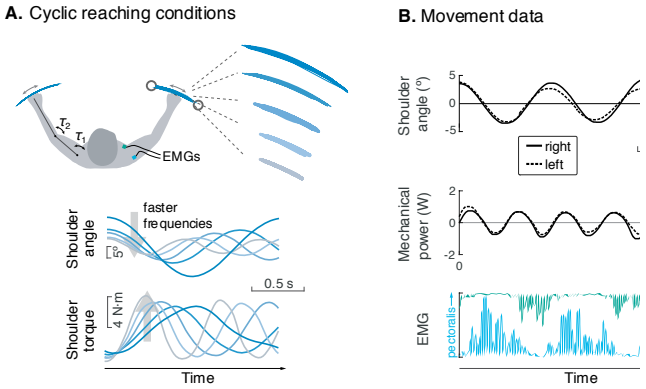

Figure 2. Experiment for metabolic cost of cyclic reaching. (A) Cyclic reaching was performed bimanually and symmetrically in the horizontal plane, primarily about the shoulders. To isolate the hypothesized force-rate cost from the energetic cost of work, movements were varied to yield fixed mechanical power, by decreasing amplitudes with increasing movement frequency. (B) Movement data included shoulder angle, mechanical power, electromyography (EMG), and (not shown) metabolic energy expenditure via expired gas respirometry.

Model predictions for force-rate hypothesis

We hypothesized that the energetic cost for reaching includes a cost for performing mechanical work, and another for the rate of force production. These costs are implemented on a simple, two-segment model of arm dynamics, actuated with joint torques. These torques perform work on the arm, at an approximately proportional energetic cost (Margaria 1976) attributed to actin-myosin cross-bridge action (Barclay 2015). The force-rate cost is hypothesized to result from rapid activation and deactivation of muscle, increasing with the amount of force and

inversely with the time duration. It is attributable to active transport of myoplasmic calcium (Bergstrom and Hultman 1988; Hogan et al. 1998), where more calcium is required for higher forces and/or shorter time durations, hence force-rate (Doke and Kuo 2007).

For the simple motion employed here, the prediction of the total energy E consumed per movement is the sum of costs for work and force-rate,

$$E = c_W W + E_{\mathrm{FR}} \tag{1}$$

where *W* is the positive mechanical work per movement, c_W the energetic cost for work, and E_{FR} is the hypothesized force-rate cost

$$E_{\mathrm{FR}} \propto \dot{F} \tag{2}$$

where $\dot{F}$ denotes the amplitude of force-rate (time-derivative of muscle force) per movement. (This cost is to be distinguished from the earlier torque-change hypothesis (Uno et al. 1989), which integrates a sum-squared force-rate over time.) During cyclic reaching, the peak force-rate $\dot{F}$ increases with both force amplitude and the frequency of cyclic movement. Here, positive and negative work are performed in equal magnitudes, and so their respective costs are lumped together into a single proportionality c_W. We assigned c_W a value of 4.2, from empirical mechanical work efficiencies of 25% for positive work and -120% for negative work (Margaria et al. 1963).

The work and force of the cyclic reaching movements about the shoulder are predicted by a simple model of arm dynamics. In the horizontal plane of a manipulandum supporting the arm,

$$T(t) = I\,\ddot{\theta}(t) \tag{3}$$

with shoulder angle $\theta(t)$, shoulder torque $T(t)$ (treated as proportional to muscle force), and rotational inertia I. Applying sinusoidal motion at amplitude A and movement frequency f (in cycle/s),

$$\theta(t) = A\cos 2\pi f t.$$

The torque is therefore

$$T(t) = -4\pi^2 I\,A\,f^2\cos 2\pi f t$$

and amplitude of mechanical power $\dot{W}$

$$\dot{W} \propto A^2 f^3 \tag{4}$$

We apply a particular movement condition, termed the *fixed power* constraint (Fig. 2A), where the average positive mechanical power is kept fixed across movement frequencies, so that the hypothesized force-rate cost will dominate energetic cost (Fig. 3A). This is achieved by constraining amplitude to decrease with movement frequency (Fig. 3B),

$$A \propto f^{-\frac{3}{2}} \tag{5}$$

This fixed power condition also means that hand (endpoint) speed, proportional to $\dot{\theta}$, should have amplitude varying with $f^{-1/2}$, and torque amplitude with $f^{1/2}$ (Fig. 3C, D).

Applying fixed power to the force-rate cost yields a predicted energetic cost. Torque-rate amplitude $\dot{T}$ with Eqn. (5) and (2) yields

$$\dot{T} = b \cdot f^{\frac{3}{2}} \tag{6}$$

where b is a constant coefficient. The proportional cost per contraction is therefore (Eqn. (2))

$$E_{\mathrm{FR}} = c_f \cdot f^{\frac{3}{2}} \tag{7}$$

where c_f is a constant coefficient across conditions. Experimentally, it is most practical to measure metabolic power $\dot{E}$ (Fig. 3a) in steady state. Multiplying E (cost per movement, Eqn. (2) by f (movement cycles per time) yields the predicted proportionality for average metabolic power,

$$\dot{E}_{\mathrm{FR}} = c_f \cdot f^{5/2}\,. \tag{8}$$

The net metabolic rate $\dot{E}$ is expected to increase similarly, but with an additional offset for the constant work cost $\dot{E}_W$ under the fixed-power constraint (Figure 3A). Finally, the metabolic energy per time associated with force-rate would be expected to increase directly with torque-rate per time $f \cdot \dot{T}$,

$$\dot{E}_{\mathrm{FR}} = c_t \cdot f \cdot \dot{T} \tag{9}$$

where movement frequency f represents cycles per time, and coefficient c_t is equal to c_f divided by b.

Experiments

We measured the metabolic power expended by healthy adults (N = 10) performing cyclic movements at a range of speeds but fixed power (Eqn. (5)). We tested whether metabolic power would increase with the hypothesized force-rate cost $\dot{E}_{\mathrm{FR}}$, in amount not explained by mechanical work. We also characterized the mechanics of the task in terms of kinematics, shoulder torque amplitude, and force-rate for shoulder muscles. These were used to test whether the mechanics were consistent with the model of arm dynamics, and whether force-rate increased as predicted (Eqns. (5-(8)). We first describe a primary experiment with fixed power conditions, followed by an additional cross-validation experiment. All subjects provided written informed consent, as approved by University of Calgary Ethics board.

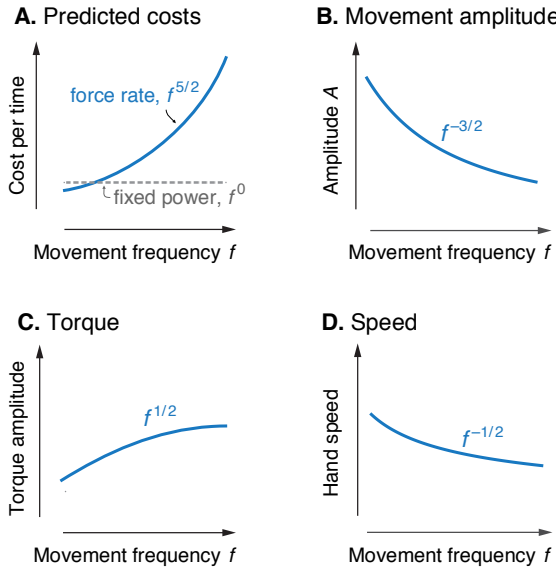

Figure 3. Predicted cost and dynamics for cyclic reaching, as a function of movement frequency f. (A.) Force-rate cost is predicted to increase with $f^{5/2}$, whereas cost for mechanical work is predicted to remain constant for fixed power conditions. (B.) Fixed power is achieved by specifying movement amplitude A to decrease with frequency, according to $f^{-3/2}$. (C.) Torque amplitudes are expected to increase modestly, with $f^{-3/2}$. (D) Peak hand speed is expected to decrease, with $f^{-1/2}$.

Subjects performed cyclic bimanual reaching movements in the horizontal plane, with the arms supported by a robotic exoskeleton (KINARM, BKIN Technologies, Inc). The exoskeleton was used to counteract gravity in a low-friction environment (with no actuator loads), and to measure kinematics, from which joint torques were estimated using inverse dynamics. Cyclic movements were between two visual targets, reachable by medio-lateral shoulder motion alone. There were however, no explicit constraints restricting free planar motions. The robot displayed a 5mm visual cursor located at the hands and visual targets 2.5 cm diameter, all optically projected onto the movement plane. A single visual cursor was displayed, as an average of right and left arm joint angles, so that the task required visual tracking of only one moving object. Timing was set with a metronome beat for each target, and amplitude by adjusting the distance between the targets. Prior to data collection, subjects completed a 20-minute familiarization session (up to 48 hours before the experiment) where they received task instructions and briefly practiced each of the tasks.

The primary experiment was to test for the predicted energetic cost for reaching, in five conditions of cyclic reaching at increasing frequency and decreasing amplitude. The frequencies

were 0.58, 0.78, 0.97, 1.17, 1.36 Hz, and amplitudes were 12.5, 8, 5.8, 4.4, 3.5°, respectively. These cyclic movements were chosen to be of moderate hand speed, with peak speeds between 0.4 – 0.6 m/s.

We estimated metabolic rate using expired gas respirometry. Subjects performed each condition for 6 minutes, analyzing only the final 3 minutes of data for steady-state aerobic conditions, with standard equations used to convert O2 and CO2 rates into metabolic power (Brockway 1987). We report net metabolic rate $\dot{E}$, defined as gross rate minus the cost of quiet sitting (obtained in a separate trial, 98.6 ± 11.5 W, mean ± s.d.).

We also recorded arm segment positions and electromyographs simultaneously at 1000 Hz. These included kinematics from the robot, and electromyographs (EMGs) from four muscles (pectoralis lateral, posterior deltoid, biceps, triceps) in a subset of our subjects (5 subjects in primary experiment, 5 in cross-validation). The EMGs were used to characterize muscle activation and co-activation.

The metabolic cost hypothesis was tested using a linear mixed-effects model of net metabolic power. This included the hypothesized force-rate cost (Eqn. 8) as a fixed effect, yielding coefficient c_f for the force-rate term proportional to $f^{5/2}$. A constant offset was included for each subject as a random effect. In addition, the force-rate cost $\dot{E}_{\mathrm{FR}}$ was estimated by subtracting the fixed mechanical work cost $\dot{E}_W$ from net metabolic power $\dot{E}$, and then compared against torque rate amplitude per time (9).

We tested expectations for movement amplitude and other quantities from kinematic data. Hand velocity was filtered using a bi-directional lowpass Butterworth filter (1st order, 12 Hz cutoff). Shoulder torque was computed using inverse dynamics, based on KINARM dynamics (BKIN Technologies, Kingston), and subject-specific inertial parameters (Winter 1990). The approximate rotational inertia of a single human arm and exoskeleton about the shoulder was estimated as 0.9 kg·m^2. The positive portion of mechanical power was integrated over total movement duration and divided by cycle time, yielding average positive mechanical power. Linear mixed-effects models were used to characterize the power-law relations for mechanical power, movement amplitude, movement speed, torque amplitude, and torque rate amplitude (Figure 3). The latter was estimated by integrating the torque rate amplitude per time (Eqn. (9)). The force-rate hypothesis was also tested by comparing $\dot{E}_{\mathrm{FR}}$ with torque rate per time (Fig 3A), assuming torque is proportional to muscle force.

Electromyographs were used to test for changes in muscle activation and co-activation. Data were mean-centred, low-pass filtered (bidirectional, second order, 30Hz cutoff), rectified, and low-pass filtered again (Roberts and Gabaldón 2008), from which the EMG amplitude was measured at peak and then normalized to each subject's maximum EMG across the five conditions. We expected EMG amplitude to increase with muscle activation, with simplified first-order dynamics between activation (EMG) and muscle force production (van der Zee and Kuo 2020). This treats the rate-limiting step of force production as a low-pass filter, so that

greater activation or EMG amplitudes would be needed to produce a given force at higher waveform frequencies. The first-order dynamics mean that EMG would be expected to increase with torque rate $f^{3/2}$ rather than torque, as tested with a linear mixed-effects model. We also computed a co-contraction index for EMG, in which the smallest value of antagonist muscle pairs was computed over time, and then integrated for comparison across conditions (Gribble et al. 2003). All statistical tests were performed with threshold for significance of $P < 0.05$.

We cross-validated the coefficient c_t by applying it to data collected in a second set of conditions with a separate set of subjects (also $N = 10$; two subjects participated in both sets). The conditions were slightly different: frequencies ranging 0.67 - 1.3 Hz and amplitudes 12.5 - 4.42°, which resulted in higher mechanical work and force-rate. The model (Eqns. (1), (9) applied the c_t coefficient identified from the primary experiment to predict metabolic cost for the cross-validation conditions, as a further test of the hypothesis.

Estimation of elastic energy storage in shoulder muscles

We estimated the resonant frequency of cyclic reaching, to account for possible series elasticity in shoulder actuation. Series elasticity could potentially store and return energy and thus require less mechanical work from muscle fascicles. We estimated this contribution from resonant frequency, obtained by asking subjects to swing their arms back and forth rapidly at large amplitudes (at least 15°) for 20 s, and determining the frequency of peak power (PWelch in Matlab). We then used this to estimate torsional series elasticity, and the passive contribution to mechanical power.

Musculoskeletal model to simulate experimental conditions

We tested whether a Hill-type musculoskeletal model could explain the metabolic cost of cyclic reaching. The hypothesized force-rate is not explicitly included in current models of energy expenditure, and would not be expected to explain the experimental metabolic cost. We therefore tested an energetics model available in the OpenSim modeling system (Seth et al. 2018; Uchida et al. 2016; Umberger 2010), applied to a model of arm dynamics with six muscles (Kistemaker et al. 2014). We used trajectory optimization to determine muscle states and stimulations, with torques from inverse dynamics as a tracking reference. Optimization was performed using TOMLAB and SNOPT (Gill et al. 2002), to minimize mean- square torque error, squared stimulation level, and squared stimulation rate. The optimized muscle states were then fed into the metabolic cost model (Umberger 2010).

Force-rate model to simulate energetic cost of point-to-point reaching

We hypothesized that force-rate minimization could predict smooth, bell-shaped velocity profiles similar to minimum-variance. We tested this by performing trajectory optimization of simulated planar, two-segment reaching movements, using the empirical force-rate coefficient c_t (Eqns. (1), (9). Again, TOMLAB and SNOPT (Gill et al. 2002) were used to optimize shoulder and elbow torques to minimize the hypothesized energy cost (Eqn. (1). The resulting hand trajectory over time was then compared the minimum-variance model (Harris and Wolpert

1998). For minimum variance, we used 7 position-space knot points (linearly spaced in time) that minimized the variance of a straight reaching movement of amplitude 30 cm, movement duration 650 ms. Matching the model of Harris & Wolpert (1998), endpoint variance was averaged over a 500 ms hold period following movement end.

Results

The rate of metabolic energy expenditure increased substantially with movement frequency, even as the rate of mechanical work was nearly constant (Fig. 4A). Subjects expended more than triple (a factor of 3.56) the net metabolic power for about twice the frequency (a factor of 2.33), with 5.32 ± 2.73 W at the lowest frequency of 0.58 Hz, compared to 18.95 ± 6.02W at the highest frequency of 1.36 Hz. As predicted, metabolic rate increased approximately with $f^{5/2}$ (Eqn. (7; adjusted R^2 = 0.50; P = 1e-8; Fig. 4a; Table 1).

Table 1. Experimental results. Linear mixed effects models were used to test model predictions from data. Listed for each quantity: predicted power law, estimated coefficient, 95% confidence interval (CI), R^2, and P-value.

Quantity	Power law	Coefficient	95 % CI	R^2	P	Inter-cept
Metabolic Power $\dot{E}$ (W)	$f^{5/2}$	6.72	(4.58, 8.86)	0.50	9.70E-9	3.93
Movement amplitude A (°)	$f^{3/2}$	5.97	(5.66, 6.28)	0.97	1.02E-39	-0.47
Peak speed amplitude (m·s^{-1})	$f^{-1/2}$	0.43	(0.39, 0.47)	0.93	6.63E-29	0.01
Torque amplitude (N·m)	$f^{1/2}$	8.34	(5.77, 10.91)	0.52	4.10E-9	1.63
Positive mechanical power $\dot{W}$ (W)	f^{0}	1.20	(0.85, 1.55)			
Torque rate per time $f\dot{T}$ (N·m·s^{-2})	$f^{5/2}$	78.93	(72.37, 85.48)	0.94	2.19E-30	46.43
EMG amplitude: Pec	$f^{3/2}$	0.17	(0.12, 0.23)	0.65	1.1E-6	0.17
EMG amplitude: Delt	$f^{3/2}$	0.20	(0.11, 0.27)	0.56	1.5e-5	0.20

Other aspects of the cyclic reaching task were as prescribed and intended (Fig. 4B-E; Table 1). Reach amplitudes decreased according to the targets, approximately with $f^{-3/2}$ (Fig. 4B). Shoulder torque amplitude and endpoint speed also changed with respectively $f^{1/2}$ (Fig. 4C; adjusted R^2 = 0.52; P = 4e-9) $f^{-1/2}$ (Fig. 4D; R^2 = 0.93; P = 7e-29). Consistent with the fixed-power condition, average positive mechanical power did not change significantly with frequency f (Fig. 4E; slope = 0.081 $\pm$ 0.13 W·s^{-1}; mixed-effects linear model with a fixed effect proportional to f^1, and individual subject offsets as random effects; P = 0.16). Amplitude of torque rate per time increased more sharply, approximately with $f^{5/2}$ (Fig. 4E), with coefficient b of 78.93 ± 6.55 CI, 95% confidence interval).

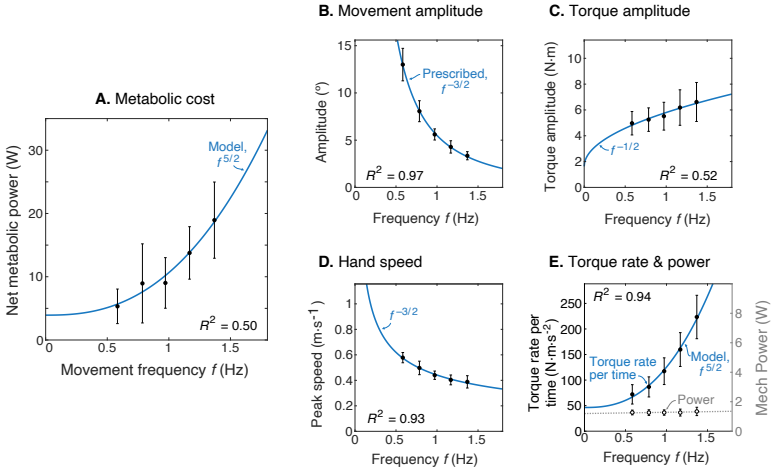

Fig 4. Experimental results as a function of movement frequency f. (A.) Net metabolic power $\dot{E}$ vs. frequency f (means ± s.d., N = 10), with predicted power law $f^{5/2}$ (solid line). (B.) Movement amplitude and prescribed target $f^{-3/2}$. (C.) Torque amplitude and prediction $f^{1/2}$. (D.) Hand speed amplitude and prediction $f^{-3/2}$. (E.) Amplitude of torque rate per time and prediction $f^{5/2}$, and mechanical power amplitude $\dot{W}$ and constant power prediction.

The net metabolic cost was also consistent with the hypothesized sum of separate terms for positive mechanical work and force-rate (Fig. 5). This is demonstrated with metabolic power as a function of movement frequency f, and as a function of force-rate per time. With positive mechanical work at a fixed rate of about 1.2 W, the metabolic cost of work was expected to be constant at approximately 5 W. The difference between net metabolic rate and the constant work cost yielded the remaining force-rate metabolic power, increasing approximately with $f^{5/2}$ (Fig. 5A). This same force-rate cost could also be expressed as a linear function of the empirical torque rate per time, with an

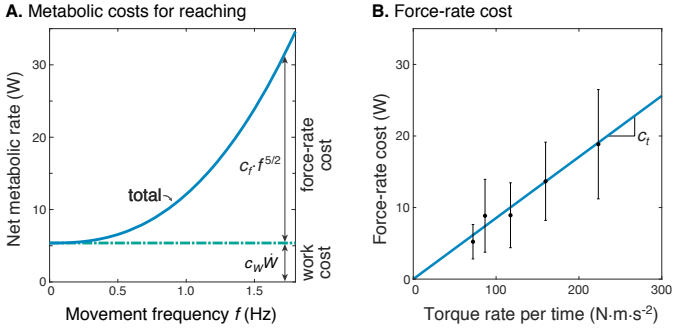

Fig. 5. Metabolic cost contributions from work and force-rate. (A.) Net metabolic rate $\dot{E}$ vs. movement frequency f for cyclic reaching, with contributions from force-rate cost ($c_f f^{5/2}$) and mechanical work ($c_W \dot{W}$). Coefficient c_f was derived from experiment (Fig. 4), whereas c_W was specified as 4.2 to model a proportional cost for positive and negative mechanical work. (B.) Force-rate cost (metabolic power $\dot{E}_{FR}$) is linearly related to amplitude of torque rate per time $f\dot{T}$, by coefficient c_t determined from part A. and Fig. 4E.

estimated coefficient of c_t=8.5e-2 (Fig. 5B; see Eqn. (9). (Joint torque is treated as proportional to muscle force, assuming constant shoulder moment arm.) In terms of proportions, mechanical power accounted for about 94% of the net metabolic cost at 0.58 Hz, and 26% at 1.36 Hz. Correspondingly, force-rate accounted for about 6% and 74% of net metabolic rate at the two respective frequencies.

Muscle EMG amplitudes increased with movement frequency (Fig. 6). Deltoid and pectoralis both increased approximately with $f^{3/2}$ (pectoralis: R^2= 0.65; P = 1.1e-6; deltoid: R^2= 0.56; P =1.5e-5), as did the co-contraction index (R^2= 0.58; P = 0.0009). This was consistent with expectations of muscle activation increasing faster than torque for increasing movement frequencies.

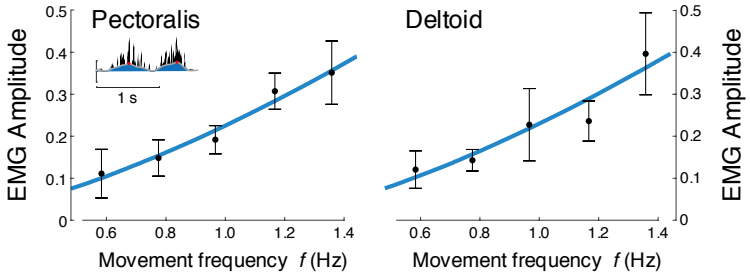

Fig. 6 EMG amplitude vs. movement frequency f during cyclic reaching. Inset figure depicts an example EMG rectified (black), filtered (blue), and amplitude (red). Pectoralis and deltoid EMGs (means ± s.d.; N = 10), with best-fit predictions curves (both $f^{3/2}$), $R^2 = 0.65$ and $R^2 = 0.56$, respectively.

Cross-validation of metabolic cost during cyclic reaching

Separate cross-validation trials agreed well with force-rate coefficients. The second group of subjects moved with slightly increasing mechanical power, and slightly higher metabolic cost (Fig. 7). But applying the cost coefficient c_t derived from the primary experiment, the model (Eqns. 1 & 8) was nevertheless able to predict cross-validation costs reasonably well (R^2 = 0.42; P = 2.7e-6).

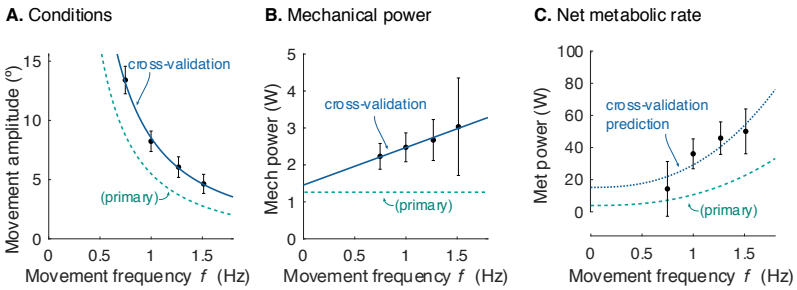

Fig 7. Cross-validation (CV) of force rate cost. (A.) Amplitude of cyclic reaching condition (compared with primary experiment) vs. movement frequency f and (B.) positive mechanical power $\dot{W}$ vs. f. (C.) Net metabolic rate $\dot{E}$ vs. movement frequency f for cross-validation (means ± s.d.; N = 10). Cross-validation conditions were such that average positive mechanical power W increased slightly with f, unlike the primary experiment. Predicted metabolic rate for CV was determined using c_t and c_W from primary experiment (solid line).

Passive elastic energy storage during cyclic reaching

The estimated natural frequency of cyclic arm motions was 2.83 ± 0.56 Hz. This suggests a rotational stiffness about the shoulder joint of about 250 N·m·rad^{-1}, if series elasticity were assumed for shoulder muscles. With passive elastic energy storage, the average positive mechanical power of muscle fascicles would decrease slightly, from about 0.5 W per arm to

0.33 W. Thus, series elasticity would cause active mechanical power to decrease with movement frequency, as energy expenditure increased.

Hill-type model does not predict experimentally observed energy cost

The Hill-type model's predicted net energy cost increased approximately linearly with movement frequency, from 33 W to 47 W. The model dramatically over-predicted the net metabolic cost for all movements (by up to a factor of 6.2), and metabolic cost rose across frequency by less than half as found experimentally (a factor of 1.42 vs. empirical 3.56). Current musculoskeletal models do not accurately predict the cost of cyclic reaching.

Force-rate cost predicts point-to-point reaching

We applied the empirical force-rate coefficient c_t from cyclic reaching (Fig. 5B) to predict discrete, point-to-point reaching. We optimized the hypothesized energy cost (Eqn. (1) for work and force-rate for a movement of fixed duration (0.65 s) and distance (30 cm) comparable to that reported previously (Harris and Wolpert 1998). The optimization cost was implemented as an integral of positive mechanical power and the absolute value of force-rate per time, with respective coefficients c_W and c_t derived from the primary experiment. The optimization yielded bell-shaped velocities (Fig. 8) similar to the minimum variance model and to empirical data (Harris and Wolpert 1998).

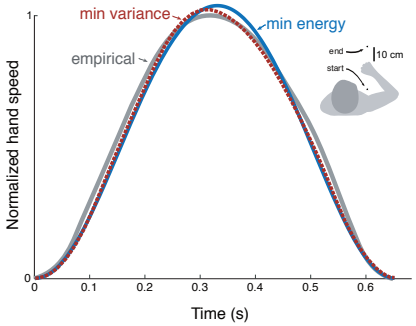

Fig 8. Hand speed trajectories for point-to-point movements predicted by energy expenditure and by minimum variance, with smooth, bell-shaped profiles. Minimum energy expenditure uses as its objective the summed costs of force-rate and work (Eqn. (1), with coefficient c_t specified from the primary experiment (Fig. 4). The minimum variance objective uses the covariance of movement error during a hold period at the target (Harris & Wolpert). Both optima use the same initial and final targets and a fixed movement duration.

Discussion

We tested whether the metabolic cost of reaching movements is predicted by the hypothesized force-rate cost. Our experimental data showed a cost increasing with movement frequency as predicted with force-rate, more so than did the mechanical work performed. The same cost model was also cross-validated with a separate set of reaching movements, and predicts smooth reaching movements, similar to the minimum variance model. We interpret these findings as suggesting the force-rate hypothesis as an energetic basis for reaching movements.

The force-rate hypothesis explains the observed metabolic energy cost increases better than by more conventionally recognized costs. For example, the cost of mechanical work cannot explain the higher cost at higher movement frequencies, because the rate of work remained fixed (Fig. 5). A possible explanation is that the energetic cost per unit of work (c_W in Eqn. 1) could increase with faster movements, due to the muscle force-velocity relationship (Barclay 2015).

But the conditions here actually yielded slower hand speeds with higher frequencies (Fig. 4D), and thus cannot explain the higher cost. Nor were our results explained by a current musculoskeletal model (Umberger 2010), which drastically overestimated the overall cost and underestimated the increases with movement frequency. The proposed force-rate hypothesis thus explains these data better than previous quantitative models or relationships.

The force-rate hypothesis was also consistent with three other observations: (1) electromyography, (2) cross-validation, and (3) point-to-point reaching. First, muscle EMGs increased more rapidly (approximately with $f^{3/2}$; Fig. 6) with movement frequency than did joint torques (approximately with $f^{1/2}$; Fig. 4C). The proposed mechanism is that brief bursts of activation require greater active calcium transport (and thus greater energy cost), because muscle force production has slower dynamics than muscle activation (van der Zee and Kuo 2020). Second, we cross-validated the primary experiment, by applying its cost coefficients (c_t and c_{W}, Fig. 5) to predict an independent set of conditions. We found good agreement between cross-validation data and the force-rate prediction (Fig. 7). The overall energy cost ($\dot{E}$ from Eqn. 1) depends on a particular combination of work, force, and movement frequency, yet only has one degree of freedom (c_t). Third, the force-rate hypothesis also explains discrete, point-to-point reaching. The characteristic bell-shaped velocity profile is predicted by optimal control, using the cost coefficients derived from cyclic movements (Fig. 8). These observations serve as falsifying tests of the force-rate hypothesis, independently predicted by a single model.

The force-rate cost is surely not the sole explanation for reaching. The optimal control approach has been used to propose a variety of abstract mathematical objective functions that can predict movement. But there may be multiple objectives that predict the same behavior. As such, careful experimentation (Harris and Wolpert 1998; Kawato 1999) was required to disambiguate minimum-variance from competing hypotheses such as minimum-jerk and -torque-change (Kawato 1999). Similarly, the present study does not disambiguate force-rate from minimum-variance, since both predict similar point-to-point movements. In fact, minimum-variance also has some dependency on effort, albeit implicitly, due to the mechanism of signal-dependent noise (Harris and Wolpert 1998). It also explains well the trade-off between movement speed and endpoint accuracy, where energy expenditure is unlikely to be important. However, the ambiguity also means that force-rate might alternatively explain aspects of movements previously attributed to minimum-variance alone. Variance and explicit energy cost could both potentially contribute to a unified objective for reaching.

Effort objectives have long been considered potential counterparts to the kinematic performance objective. For example, the integrated squared muscle force or activation or torque-change all emphasize effort and arm dynamics as explicit features for reaching (Uno et al. 1989). Effort is also important for selection of feedback control gains (Kuo 1995; Todorov and Jordan 2002), adaptation of coordination (Emken et al. 2007), identification of control objectives from data (Vu et al. 2016) and determination of movement duration (Shadmehr et al. 2016). In many such cases, effort was considered an abstract optimization variable, but was not seriously considered to have a physiological and measurable representation as metabolic energy expenditure. However, the adaptation of metabolic cost during adaptation (Huang et al.

2012) and the effect of metabolic state on reaching patterns (Taylor and Faisal 2018) strongly suggest a role for energy in reaching. The present study offers a potential means to unify effort in optimal control predictions with metabolic energy expenditure.

There is a measurable and non-trivial energetic cost for cyclic reaching. Even though the arms were supported by a planar manipulandum, at a movement frequency of 1.5 Hz, we observed a net metabolic rate of about 19 W. For comparison, the difference in cost between continuous standing and sitting is about 24 W (Mansoubi et al. 2015), making the reaching task nearly as costly as standing up. And per reaching movement, the metabolic cost (at two movements per cycle) was about 7 J. This may be sufficiently high for the nervous system to prefer economical ways to accomplish a reaching task.

There are several limitations to this study. One is that energetic cost was experimentally measured for the whole body, and not distinguished at the level of the muscle. Force-rate was also estimated from joint torque and not from actual muscle forces. We therefore cannot eliminate other physiological processes as possible contributions to the observed energy cost. In addition, the hypothesized cost ($\dot{E}_{FR}$) is thus far a highly simplified, conceptual model for a muscle activation cost. More precise mechanistic predictions of this cost would be facilitated with specific models for muscle activation, myoplasmic calcium transport, and force delivery are needed (e.g., Baylor and Hollingworth 1998; Ma and Zahalak 1991). Additional experiments could test the force-rate hypothesis further, and additional models could extend the mechanistic basis for this cost.

The force-rate hypothesis suggests a substantial role for effort or energy expenditure in upper extremity reaching movements. Some form of effort cost is often employed to examine selection of feedback gains or muscle forces, and even generally expected for optimal control problems where maximal-effort actions are to be avoided (Bryson and Ho 1975). And in the experimental realm, energy expenditure is regarded as a major factor in animal life and behavior (Alexander 1996), even to the small scale of a single neural action potential (Sterling and Laughlin 2017). Under the minimum-variance hypothesis, reaching seems unusually dominated by kinematics. But our results suggest that metabolic energy expenditure may have been shadowed by the minimum-variance hypothesis, because it makes similar predictions for point-to-point movements. There is need to both quantify and test the force-rate hypothesis more specifically. Nonetheless, there is a meaningful energetic cost to reaching that can also explain the smoothness of reaching motions.

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