The Trajectory of Human Wrist Movements

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SUMMARY AND CONCLUSIONS

- 1. To determine the form of human movement trajectories and the factors that determine this form, normal subjects performed wrist flexion movements against various elastic, viscous, and inertial loads. The subjects were instructed with visual and auditory feedback to make a movement of prescribed amplitude in a preset period of time, but were free to choose any trajectory that fulfilled these constraints.
- 2. The trajectories were examined critically to determine if they corresponded to those which would minimize the root mean square (RMS) value of some kinematic variable or of energy consumption. The data agreed better with the trajectory that minimized the RMS value of jerk (the third derivative of length) than that of acceleration. However, systematic deviations from the minimum jerk predictions were consistently observed whenever movements were made against elastic and viscous loads.
- 3. Improved agreement could generally be obtained by assuming that the velocity profile varied according to a normal (Gaussian) curve. We conclude that minimization of jerk is not a general principle used by the nervous system in organizing voluntary movements, although movements may approach the predicted form, particularly under inertial loading conditions.
- 4. The EMG of the agonist muscles consisted of relatively simple waveforms containing ramplike increases and approximately exponential decays. The form of the movements could often be predicted quite well by using the EMG as an input to a linear second-order model of the muscle plus load. Rather than rigorously minimizing a kinematic variable or energy consumption, the nervous system may generate simple wave-

forms and adjust the parameters of these waveforms by trial and error until a trajectory is achieved that meets the requirements for a given load.

INTRODUCTION

With little conscious thought we reach out quickly and accurately to touch an object within the range of our arms. What strategy are we using in this common task? If we are faced with constraints concerning the distance and time available for a movement, is there some parameter of the movement that we try to optimize? Recently Hogan and Flash (15) suggested that movements are carried out so as to minimize the square of a parameter called "jerk" over the course of a movement. Jerk is the third derivative of length, velocity, and acceleration, being the more commonly studied first and second derivatives.

Others have suggested that energy consumption of the muscles might be optimized (13, 21). It seems plausible from common experience that we try to move in a smooth fashion so that there is little jerkiness or that we try to move in a relatively efficient fashion so as to minimize energy costs, but there has been no definitive experimental test of these ideas. Nor has there been any indication how the nervous system might compute the trajectory of a movement so as to optimize a particular parameter.

Although the nature of the command signals for limb movements is still uncertain, saccadic eye movements are known to be produced by a burst of activity, whose duration is proportional to the saccade amplitude (8, 23). The burst is followed by activity appropriate to the maintenance of the final position. Separate parts of the brain may be involved in producing the two parts of the

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- i 1 1 1 t - : f movement (7). Similarly, a pulse-step model has been suggested for brief isometric contractions of limb muscles (9, 10). Still other views have been suggested for the neural control of movement in which the basal ganglia and cerebellum have been likened to a ramp generator and a pulse generator, respectively (16, but see 4, 5).

Our objective was to test various theoretical possibilities in as simple an experimental situation as possible. For this purpose we asked normal human subjects to make wrist flexion movements between two fixed positions in a preset time interval. Visual feedback was given to the subject so that he could "improve" his performance with practice. Movements were made against a linear DC motor whose dynamic characteristics could be modified by feedback to simulate a variety of loads.

The reason for varying the load was that, if the mean square or root mean square (RMS) value of some kinematic parameter such as acceleration or jerk were being minimized over the course of the movement, the form of the movement should be independent of load (24). However, if some derived quantity such as energy consumption were being minimized, the form of the movement should depend on the type of load against which the movement was taking place. Finally, if the nervous system used a preset plan, such as a burst followed by a period of maintained activity, this pattern should be evident under a variety of conditions, although the parameters of the EMG pattern might vary systematically with the magnitude and nature of the load.

In addition, the amplitude and time allowed for the movement were varied. Again, minimization of some kinematic parameter would require that the form of the movement should remain the same except for scaling factors associated with the magnitude and duration of the movement. In contrast, energy minimization might require that the trajectory of the movement change in a more complex way.

METHODS

Four adult male subjects between the ages of 27 and 47 yr of age were studied. The aim and methods used were explained to each subject and

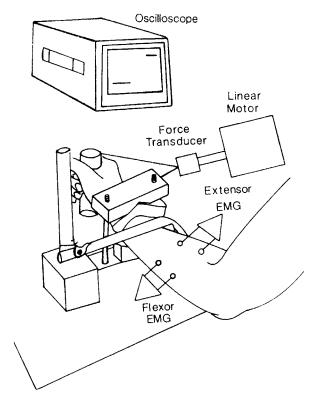


FIG. 1. Experimental arrangement for studying wrist flexion movements. Wrist position was displayed on an oscilloscope and subjects were asked to move the trace from the bottom line to the top line in the time required for oscilloscope beam to cover the gap between these two lines. Load against which the subject worked could be varied by changing the feedback of length, velocity, and acceleration to the linear motor. Force and surface EMG from wrist flexor and extensor muscles were also measured.

each subject gave informed consent. The right forearm was fixed at the wrist in such a way that the wrist flexor muscles and tendons were not restricted (Fig. 1). Milled plastic pieces at the top and bottom of the subject's wrist could be screwed together to secure the wrist, while foam inserts were used to maintain the subject's comfort. A padded bar (Fig. 1) provided a third point of fixation and prevented vertical or lateral movements of the forearm. Thus the forearm remained well stabilized during the wrist flexion movements.

The subject held a round plastic cylinder that was connected via either inelastic threads or a rigid coupling to a linear motor that generated a preset force. The presence of a background force tended to compress the soft tissue of the hand somewhat so that the extent of the hand movements was virtually the same as that of the armature of the linear motor. When using the threads, movements of the load could only be made by exerting a net flexor torque. With the rigid coupling net extensor torques could be transmitted to

the load to brake its movement, so the effect of the coupling on EMG patterns and the form of the resultant movements could be studied.

Surface EMG electrodes were placed over the motor points of the wrist extensor and wrist flexor muscles. Usually flexor carpi ulnaris (FCU) was used. but similar records were obtained with flexor carpi radialis (FCR). The EMG signals were amplified and recorded with a pass band of 10–10,000 Hz. For averaging, the signals were rectified and low-pass filtered with a high-frequency cutoff of 100 Hz.

The force exerted by the muscles was measured with a force transducer in series with the coupling and the linear motor contained length and velocity sensors. The fidelity of the velocity sensor was regularly checked by differentiating the position record numerically. Acceleration was measured by differentiating velocity electronically and was also checked by numerical differentiation of the position or velocity traces. The amount of length, velocity, and acceleration feedback was adjusted using 10-turn potentiometers to simulate elastic, viscous, or inertial loads, respectively, as described below.

Determination of the effective load

The magnitudes of the applied loads were determined from the movements produced by subjects during experiments as follows. The load was assumed to be of the form

$$F = Kx + Dv + Ma + C \tag{1}$$

where x, v, and a are the position, velocity, and acceleration of the load and K, D, M, and C are the effective values of stiffness, viscosity, mass, and constant force, which were determined by the method of least mean squares (27).

The results of this procedure are shown in Fig. 2. The forces recorded during actual movements are shown and are displaced above the axis by the amount of the constant (bias) force that the subject had to maintain to hold the starting position. The elastic component of the load will produce a force proportional to the sigmoid shape of the length changes (see RESULTS); the viscous component will produce a force proportional to the bell-shaped profile of the velocity trace and the inertial component a force proportional to the biphasic acceleration trace.

The effective stiffness of the "elastic load" in Fig. 2A was 2.9 N/mm, which was produced by using length feedback. The viscous and inertial components are minimal, since the viscosity and inertia of the motor were effectively cancelled by adding a predetermined amount of positive velocity and acceleration feedback. Similarly, the "viscous" load of Fig. 2B had an effective viscosity of 670 Ns/m with very little contamination from

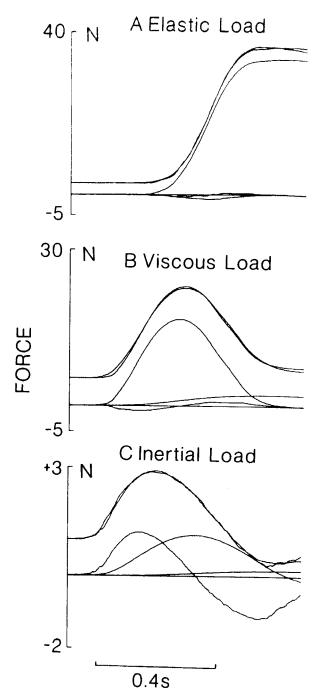


FIG. 2. Effective load was determined by a least-mean-squares fitting procedure. In each part of the figure the best-fitting elastic (proportional to length), viscous (proportional to velocity), and inertial (proportional to acceleration) components are shown. A constant force was also needed to maintain initial position. When this was added to the sum of the other 3 components, the result agreed well with experimentally observed force, as shown by excellent superposition of upper 2 traces in each part of figure. Only the elastic component was sizable in A, and only the viscous component in B, but both viscous and inertial components contributed substantially to the "inertial" load in C. Movement time = 0.4 s; handle coupled to motor with a fixed linkage.

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elastic and inertial components. The "inertial load" of Fig. 2C had a large component proportional to acceleration (effective inertia = 11 kg), although the viscous component was also substantial. The viscous component could not be further reduced for an inertial load of this size by feedback without the control system showing some instabilities. We studied a range of elastic loads from 0.1 to 3.5 N/mm, a range of viscous loads from 100 to 700 N.s/m, and a range of inertial loads from 1 to 12 kg.

The filtering necessary to stabilize the feedback system introduces some delays. In addition, because of static friction force will rise before the movement actually begins. Friction is a nonlinearity that is difficult to deal with adequately, but we have shifted the force traces to the right by 24 ms before using the fitting procedures shown in Fig. 2. This value corresponds to the empirically determined delay. The sum of the four components (elastic, viscous, inertial, and constant) is also shown in each part of Fig. 2 and it superimposes well on the experimentally measured force. For example, the residual RMS deviations are only 0.26 N in Fig. 24.

Experimental procedure

In most experiments the subjects viewed an oscilloscope that displayed wrist position. The oscilloscope had markings indicating the desired initial and final positions. As the sweep moved across the oscilloscope face, subjects attempted to move the handle so that the beam moved from the initial to the final position during the interval represented by the gap between the two marks. The desired amplitude of movement could be changed by altering the amplifier gain while the desired movement time could be varied by changing the sweep speed. The time interval between successive movements was set at a value for each series that allowed the subject to complete the movement and return the handle to the starting position easily before the next movement was to be initiated (typically 4–8 s).

A loud speaker also produced three clicks to signal "get ready," "go" and "stop." At the first click the sweep of the oscilloscope was initiated. At the second click the oscilloscope beam reached the end of the marking for initial position and at the third click the beam reached the beginning of the marking for final position. With this combination of auditory and visual signals and some practice (typically 5–15 repetitions) to develop a rhythm, subjects could make consistent movements of approximately the correct amplitude and duration. In some experiments the visual feedback was turned off after the trial period. Subjects typically made movements of the same

form, but errors in the amplitude and duration of the movements were greater.

After the trial period, subjects made about 20 movements against a given load. The length, velocity, acceleration, force, flexor EMG, and extensor EMG were recorded on magnetic tape, together with the digital pulses that were used to generate the clicks in the loud speaker. The first pulse was also sent to a general-purpose laboratory computer (Digital Equipment Corp., PDP 11-34), which was programmed for on-line signal averaging. This average, together with display of the individual trajectories on a storage oscilloscope, provided confirmation of the quality of the data at the time of the experiment.

Further data analysis

After the experiment the data could be replayed from tape and stored on a hard disk. Movements could be selected for averaging from the disk, based on preselected parameters of the movement. This reduced the variability of the movements considerably and permitted more accurate, quantitative evaluation of the form of the trajectory (see Fig. 3 in RESULTS). The following forms were considered:

MINIMUM ACCELERATION. If a movement is made from an initial resting position x_0 at time t_0 to a final resting position $x_0 + X$ at $t_0 + T$ (i.e., a movement of magnitude X is made in time T), it can be shown by standard methods from the calculus of variations (see 28) that the form of movement that minimizes the RMS acceleration over the course of the movement is

$$x = x_0 + 3 X(t - t_0)^2 / T^2 - 2 X$$

$$\times (t - t_0)^3 / T^3, \quad t_0 < t < t_0 + T \quad (2)$$

Four parameters must be determined: the resting position x_0 , the time of initiating the movement t_0 , the extent of the movement X, and the duration of the movement T. A nonlinear gradient search algorithm was used to find the values that minimize the mean square error of the predicted position from the experimentally measured position trajectory (see the APPENDIX in 29 for further details of the algorithm).

MINIMUM JERK. If instead a movement of the same magnitude and duration is made so as to minimize the RMS value of jerk (the third derivative of position) over the course of the movement, the form can again be predicted by the calculus of variations (14, 28) for movements that start and end at rest, namely for $t_0 < t < t_0 + T$

$$x = x_0 + 10X(t - t_0)^3/T^3 - 15X(t - t_0)^4/$$
$$T^4 + 6X(t - t_0)^5/T^5 \quad (3)$$

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The same four parameters are required and can also be determined by a gradient search algorithm so as to minimize the RMS error of the predicted position from the experimentally measured position.

NORMAL (GAUSSIAN) CURVE. The velocity profiles often looked "bell-shaped," so another possibility is that the velocity is in the form of a normal or Gaussian curve given by

$$v = \frac{X}{\sqrt{(2\pi)\sigma}} e^{-(t-t_1)^2/(2\sigma^2)}$$
 (4)

and the position would then be given by

$$x = x_0 + \frac{X}{\sqrt{(2\pi)\sigma}} \int_0^1 e^{-(t-t_1)^2/2\sigma^2} du.$$
 (5)

Again there are four parameters to be determined by a gradient search algorithm to minimize the RMS deviations from Eq. 5). X and x_0 have the same meaning as before; t_1 is the midpoint of the movement and σ represents the "standard deviation" of the velocity profile.

ABSOLUTE OR BIEXPONENTIAL CURVE. Another form that was tried was the biexponential function, given by the following expressions for velocity and position

$$v = (0.5X/\tau)e^{-|t-t_1|/\tau} \tag{6}$$

$$x = \frac{x_0 + 0.5Xe^{(t-t_1)/\tau}}{x_0 + X - 0.5Xe^{(t_1-t_1)/\tau}}, \quad t \le t_1$$
(7)

where τ is the time constant of the exponential function. Four parameters must again be determined by a gradient search algorithm.

SECOND-ORDER MODEL. Finally, we assumed that the muscle plus load could be modeled as a linear second-order system with the EMG as input and length as output. The methods used are somewhat more complex and are developed in the APPENDIX.

RESULTS

Figure 3A shows a series of movements against a spring load of 2.7 N/mm. The subject tried to complete the movement of 12 mm in a time of 0.4 s, as indicated by the bar at the bottom of the figure. The distance from the handle to the axis of rotation of the wrist was $\sim 9 \text{ cm}$, so this movement represents a rotation of 8° . Because of the small angle involved, the linear movements of the motor were essentially proportional to the angular movements of the wrist. Since we measured the linear movement in millimeters, these values will be used throughout,

rather than values in degrees. The subjects made movements that corresponded fairly well on average to the magnitude and duration specified (Fig. 3B), despite the substantial variability observed for individual traces.

Much of the variability arises in the timing of the movement with respect to the getready signal for what is essentially a repetitive, auditory, and visual reaction time. On a few trials the movement was substantially too fast or too slow or appeared to occur as multiple movements, rather than a single, continuous movement.

On the right of Fig. 3 selected traces have been lined up with respect to the midpoint of the movement for that particular trial (position-locked), rather than to the get-ready signal (time-locked). There is still some variability in the amplitude of the movement, but the timing of the movements are quite similar and the form of the movement and its derivatives can be specified more accurately by averaging the position-locked traces and the corresponding velocity and acceleration traces. In general, the movements were faster (reaching higher peak velocities) for the selected position-locked averages than for the time-locked averages. Averaging traces in which the time of the peak velocity varied would obviously reduce the peak value.

Fitting the movement kinematics

The position-locked average of position, velocity, and acceleration traces have been reproduced in both halves of Fig. 4. These traces have been compared with the predictions of different strategies that might have been used to produce the movement. Figure 4A compares the experimental data with a "minimum acceleration" and a "minimum jerk" prediction (i.e., where the RMS value of the second or the third derivative of position has been minimized over the course of the movement).

Both predictions fit the position trajectory well with residual RMS deviations of 0.27 mm (minimum acceleration) and 0.24 mm (minimum jerk). However, some deviations are apparent in the velocity and acceleration profiles; Eq. 2) for minimizing RMS acceleration is a third-order polynomial, so differentiating to obtain velocity will give a second-order polynomial (parabola). Differen-

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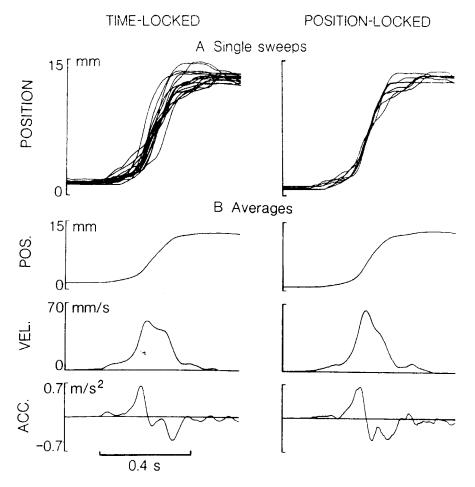


FIG. 3. A: trajectories of individual movements have been superimposed, either locked in time to the get-ready signal (left) or relative to the midpoint of the movement (right). Movements that were much faster or slower than the average were also excluded from the right-hand side. B: average position, velocity, and acceleration of sweeps on left-hand side and those on right-hand side have been averaged separately to specify the form of the movement more accurately. Requested movement time = 0.4 s, as indicated by time bar at bottom. Thread was used as a linkage to the handle.

tiating twice will give an acceleration, which increases abruptly at the beginning of the movement, then declines linearly before returning abruptly to zero at the end of the movement. In fact, the experimental data rise smoothly and decay smoothly; differences from the prediction are particularly evident in the acceleration trace.

Equation 3 for minimizing RMS jerk is a fifth-order polynomial so velocity should follow a fourth-order polynomial and acceleration a third-order (cubic) polynomial, which are substantially smoother than for Eq. 2). The agreement is better, but deviations are still evident in the velocity trace and more obvious in the acceleration trace. The form of the cubic equation is such that the peak acceleration should occur about one-

quarter of the way through the movement and the peak deceleration at about three-quarters of the way through the movement (exact values are given in the DISCUSSION). In fact, the peaks in acceleration and deceleration are larger than predicted and occur closer to the midpoint of the movement than predicted. Such deviations were consistently seen with elastic loads.

In addition to these kinematic predictions other possible forms of movement were considered. For example in Fig. 4B we tested the possibility that the length followed a curve given by Eq. 5) which is the integral of the normal or Gaussian density function of statistics. As for the minimum acceleration and minimum jerk predictions, there are four free parameters, although the interpretation

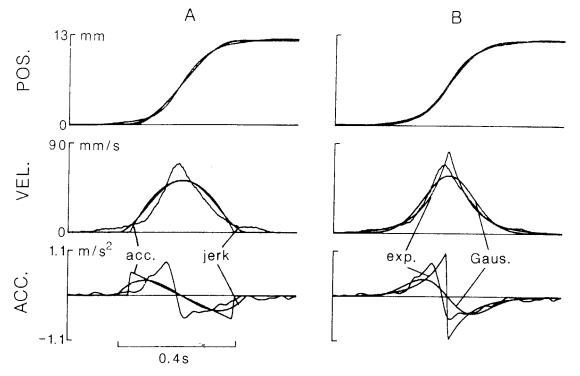


FIG. 4. The same averages of position, velocity, and acceleration are shown in both parts of this figure. Superimposed on the data are predicted trajectories that would minimize root mean square acceleration (acc) or jerk (A) or in which the velocity would follow a Gaussian (Gaus) or biexponential (exp) form (B). Length traces superimpose well, but deviations are evident in the velocity and acceleration traces. Movement time, 0.4 s; elastic load = 2.7 N/mm with thread linkage. Position-locked averages are used in this and all later figures.

of some of the parameters is rather different, as described in METHODS. The fit to the trajectory is even better with an RMS error of only 0.16 mm. This also leads to a better fit of the velocity and acceleration profiles, although the acceleration and deceleration peaks still occur closer to the midpoint of the movement than predicted.

A final form of curve is obtained from the biexponential function and is also shown in Fig. 4B. The fit is even better in this example (an RMS deviation of 0.10 mm), but the predicted peaks in acceleration and deceleration are somewhat too large and occur right at the midpoint of the movement. The systematic deviations are therefore in the opposite direction to those obtained with the other curves.

In 30 trials in which average movements against spring loads were computed, a Gaussian curve gave the best fit on 20 of the 30 trials, the minimum jerk predictions were best on five and the biexponential on five. If we assign the numbers 1-4 to curves that gave the best to worst fit in terms of RMS

deviations in the position traces, the average order was Gaussian (1.4), jerk (2.2), biexponential (2.9), and acceleration (3.5). Although somewhat different parameters were obtained when we fitted time-locked averages rather than position-locked averages, the same systematic deviations and order in terms of goodness of fit were obtained with the various functions tested.

In fitting a biexponential or a Gaussian curve to the trajectory, we do not want to imply that the nervous system plans the trajectory so as to produce one or other of these mathematical functions. However, since these functions can produce a fit as good or even better than that of the minimum jerk prediction, the data certainly provide no grounds for arguing that the nervous system tries to minimize a particular kinematic variable such as jerk (cf., 15).

Effect of movement amplitude, duration, and visual feedback

Figure 5 shows the effect of changing the movement amplitude. A weaker spring load

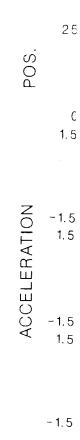


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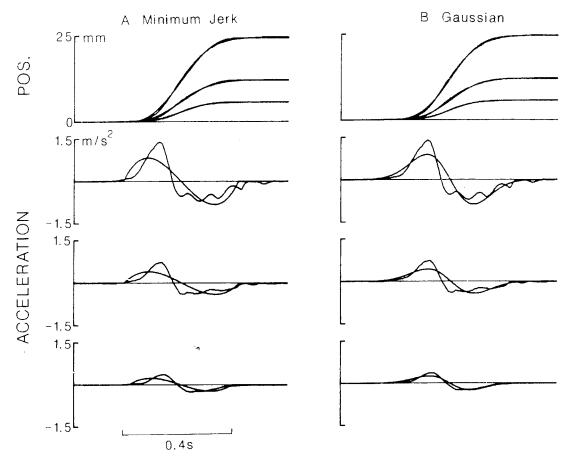


FIG. 5. Effect of movement amplitude was studied on the goodness of fit obtained by predictions based on minimizing jerk (A) and a Gaussian curve (B). The position traces are superimposed but the acceleration traces for the large, medium, and small movements are shown separately in successive rows of the figure. Predictions fit the length traces well, but the same systematic deviations are seen in all acceleration traces. Gaussian curves generally fitted better than the minimum jerk predictions. Movement time 0.4 s; fixed linkage; elastic load = 0.70 N/mm.

of 0.7 N/mm was used so that the subject could make larger movements and three different sizes of movement are illustrated. All movements have approximately the same form, so clearly the trajectory is not determined by the limits of muscle activation. An approximate scaling of movements with target amplitude has been shown in many previous studies (see Ref. 25 and references to earlier work in that paper).

The Gaussian curve does rather better than the minimum jerk prediction in all parts of Fig. 5, but the movements are clearly asymmetrical with a peak acceleration greater than the peak deceleration (see also 24). This asymmetry could arise simply from muscle properties, since the rate of rise in force during a twitch is much faster than the rate of decay. If this is the cause, the asymmetry should become greater the faster the

movement and be less prominent for slower movements.

Figure 6 tests this point by comparing the trajectory of movements at three different speeds. Again, there is an approximate scaling of movement parameters with speed, as described previously (see Ref. 30 and references to earlier studies in that paper). However, the slowest movement is probably the most asymmetric, just the opposite of what was suggested from muscle properties above.

Another frequent observation is that the narrower the target zone, the more asymmetric movements become (20). In our experiments no target zone was specified as such, but we examined this possibility by asking the subjects to make some movements without visual feedback so as to eliminate any specification of target zone completely. As shown in Fig. 7, the movement without vi-

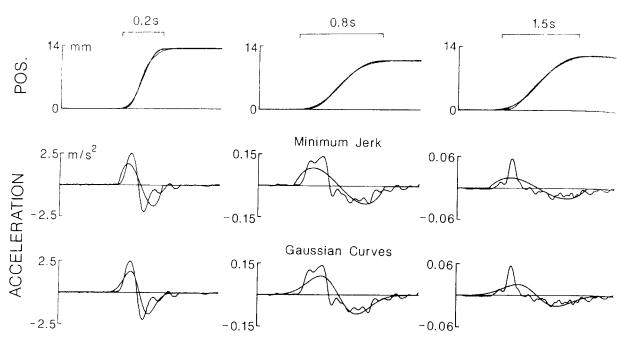


FIG. 6. The same amplitude of movement as in Fig. 4 was performed as quickly as possible (A), with a duration of 0.8 s (B), or with a duration of 1.5 s (C). The position traces have been fitted by minimum jerk predictions or by predictions based on Gaussian curves. Deviations are still evident in the acceleration traces, which remain asymmetric for all speeds of movements. Elastic load = 1.2 N/mm; thread linkage.

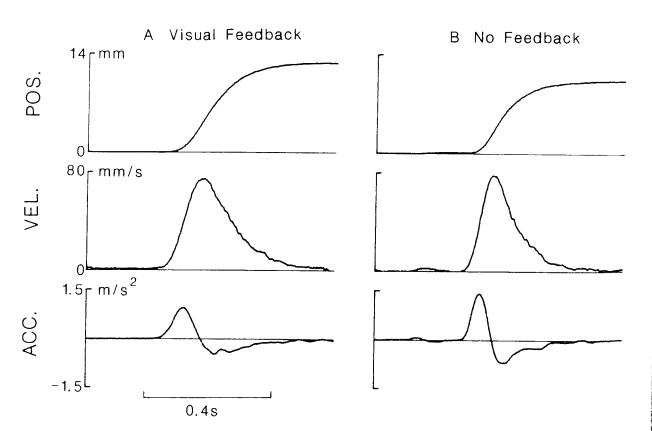


FIG. 7. In the absence of visual feedback (B) this subject made somewhat smaller, but faster movements than when feedback was present (A), but the form of movement was similar and asymmetries in velocity and acceleration traces were still present. Elastic load = 0.70 N/mm; fixed linkage; movement time = 0.4 s.

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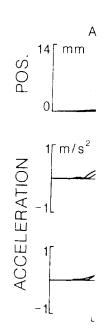


FIG. 8. Com ity = 620 Ns/n Gaussian curve acceleration rec

sual feedback in this subject tended to be smaller but faster than the one with visual feedback, but both show some degree of asymmetry.

Other types of loads

Another possibility is that the deviations from symmetry and in the timing of the acceleration and deceleration peaks (see discussion of Fig. 4) are due to the use of spring loads. Most previous studies have used torque motors which, together with the limb itself, constitute a predominantly inertial load (6). Figure 8 compares data from movements against elastic (A), viscous (B) and inertial (C) loads. The viscous load produced movements with the same asymmetries and timing errors mentioned above for the elastic load. On average, the order in goodness of fit was Gaussian (1.4), jerk (1.8), acceleration (3.1), and bi-exponential (3.7), where the best fit was assigned a 1 and the worst fit a 4. The fit is really quite good for the inertial load, both with the minimum jerk prediction and the Gaussian curve. In this figure and on average the minimum jerk prediction was somewhat better with the order being jerk (1.4), Gaussian (2.1), acceleration (2.6), biexponential (4.0).

A final possible cause of the deviations from predictions was the type of linkage used in these studies. By using an inelastic thread only net torque generated by wrist flexion would be transmitted to the force transducer. In contrast, natural movements are often generated by the combined action of antagonistic pairs (12, 17, 19), so a few experiments were done with a rigid coupling between the handle and the linear motor. Then, wrist flexors and wrist extensors could be effective both in moving and stopping the load. Figure 9 illustrates movements against elastic and viscous loads (i.e., the conditions where deviations from predictions were observed in Fig. 8), when the rigid coupling was used. Asymmetries between acceleration and deceleration are still evident.

EMG patterns

Also shown in Fig. 9 are the rectified and averaged EMGs from the flexor and extensor muscles. The form of the flexor EMG varies with the nature of the load, as would be expected. A substantial EMG and force must be used to hold the muscle at its final length with a spring load, but no EMG or force is required to maintain the final position against a viscous load. Antagonist EMG

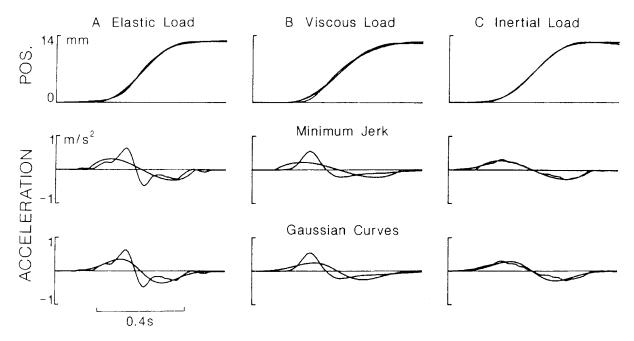


FIG. 8. Comparison of movements against an elastic load (A) (stiffness = 1.2 N/mm), a viscous load (B) (viscosity = 620 Ns/m, or an inertial load (C) (inertia = 5.5 kg). The minimum jerk predictions and those based on Gaussian curves have been fitted to the data in each part of the figure. Systematic deviations are evident for the acceleration records in A and B, but not in C. Movement time, ~ 0.5 s.

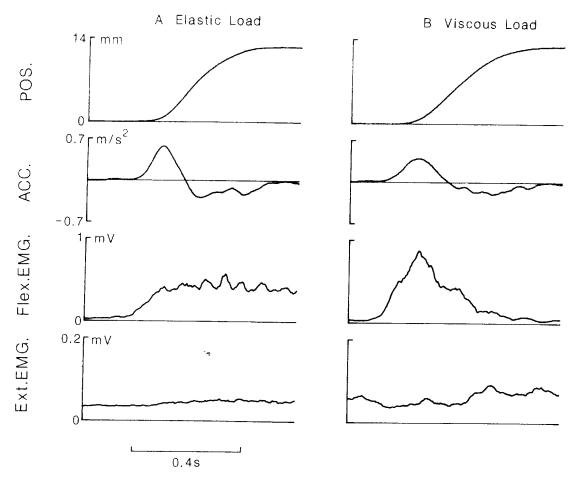


FIG. 9. Comparison of movements against elastic (A) (stiffness = 2.5 N/mm) and viscous (B) (viscosity = 680 Ns/m) loads, as in Fig. 8. The rectified and averaged flexor and extensor surface EMGs are also shown for each movement. The extensor EMG was small for the flexion movements in this figure, where a rigid coupling to the handle was used and virtually absent for movements in other experiments using thread as a linkage. Movement time, 0.4-0.5 s.

would not be required at all for flexion movements against a spring load, since these movements require an increasing flexion force. All that is observed is a small amount of cocontraction to stabilize the position of the load. A small amount of extensor EMG might be useful to speed the deceleration of the limb against viscous loads and some activity is seen.

The flexor and extensor EMGs are plotted with different scales (a factor of 5), although the maximum voluntary surface EMG from the two muscle groups was comparable. Thus the low level of extensor EMG observed resulted from weak activation of the extensor muscles, rather than from poor recording of the EMG activity. In the experiments using thread as a linkage, the extensor EMG was even lower and was generally neg-

ligible. Thus the nervous system can modify the pattern and balance of EMG to produce movements against different loads and linkages. Since deviations are observed under a variety of conditions from the patterns expected if RMS jerk were minimized, we must conclude that minimizing jerk is not a general organizing principle used by the nervous system in producing movements.

To produce a similar movement against a variety of loads, quite different patterns of EMG were required, as already pointed out in Fig. 9. The relationship between EMG and force under isometric conditions is often well fitted by a second-order model (18, 26). Indeed, for movements against elastic loads, a linearized model of the muscle and load indicates that a second-order model should also be applicable (see the APPENDIX) and the



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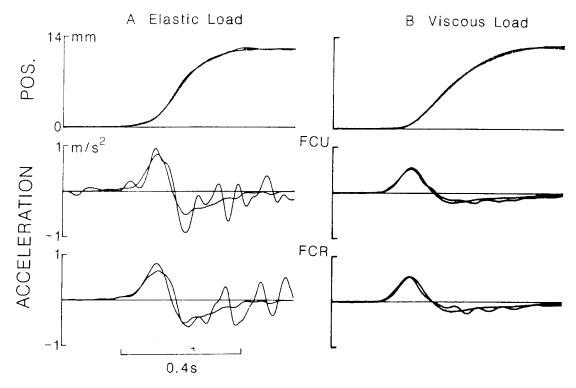


FIG. 10. Predictions for the form of movement from the EMG recorded over the flexor carpi ulnaris (FCU) or flexor carpi radialis (FCR) muscles using a linear, second-order model of the muscle and load. The timing of peaks and asymmetries in the acceleration traces were well fitted using either EMG, although there are some nonsystematic (random) errors due to the "noisiness" of EMG recordings, even when rectified and filtered (see Fig. 9). Data for the viscous load is the same as in Fig. 8B, so goodness of fit can be compared. Elastic load in A = 2.1 N/mm with a rigid coupling.

form of the EMG, which we will refer to as n(t), should be given by

$$n(t - t_d) = kx(t) + dv(t) + ma(t)$$
(8)

Equation 8 is of the same basic form as Eq. 1 except that we have explicitly included the time delay (t_d) for excitation-contraction coupling and we have used small letters, since the values k, d, and m now refer to combined properties of the muscle and load, rather than simply the stiffness, viscosity, and inertia of the external load. To compare the results with those of previous sections, we have actually solved for the position x(t) and its derivatives, velocity v(t) and acceleration a(t), using the EMG as an input (see APPEN-DIX). We have also eliminated the constant Cby setting the position and EMG arbitrarily to zero at the beginning of the trace, so that there would be the same number of free parameters $(k, d, m, and t_d)$ as in previous predictions.

The results of this fitting procedure are shown in Fig. 10 for elastic and viscous loads. Since more than one agonist muscle was involved, separate fits are shown based on the

EMG from either FCU or FCR. Since the antagonists were not modulated to a significant degree (see extensor EMG in Fig. 9), they were ignored in the analysis. The fit for the movement against the elastic load was comparable to those shown previously (RMS) deviation = 0.12 mm for FCU and 0.13 mm for FCR). However, the nature of the deviations was quite different. The residual errors in the acceleration trace, for example, show random oscillations that are probably due to the sampling limitations using surface EMG and physiological tremor (see DISCUSSION), rather than the systematic deviations of previous predictions in the timing of peaks and the asymmetry of the movement.

The same fitting procedure was also applied to the viscous load, although theoretically a third-order, rather than a second-order system should have been used. The resultant prediction for the movement was very good (RMS deviations = 0.15 mm for FCU and 0.11 mm for FCR) and the timing and asymmetry in the acceleration trace are well accounted for. Thus, even though the form of EMG is quite different for the elastic

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and viscous loads (Fig. 9), the nervous system has clearly modified it in a way that produces a rather similar form of movement (24). The asymmetry and timing of peaks deviates from the minimum jerk trajectory or other simple functions used in previous sections, but is predictable from the EMG output and the mechanical properties of the muscle and its load under conditions of elastic and viscous loads. These deviations are less obvious with inertial loads. The implications of these results will now be discussed.

DISCUSSION

In the INTRODUCTION several possible strategies were outlined that could be used to determine the trajectory of human wrist movements: 1) the RMS value of a kinematic variable, such as acceleration or jerk, could be minimized; 2) energy consumption by the muscles could be minimized, or 3) the task of the nervous system could be facilitated by combining simple functions such as pulses, ramps, and steps to produce the desired trajectory. In the RESULTS we have tried to test some of these possibilities systematically, and they will be evaluated in separate sections below.

Minimization of kinematic variables

A rationale can be proposed for minimizing several kinematic variables, or, more specifically, the integral of the square of these variables. The reason for squaring a variable such as acceleration, is that the integral of acceleration over the course of a movement is simply the velocity, evaluated at the beginning and end of the movement. If the movement begins and ends at rest, the integral will always be zero. Minimizing the variable squared over the course of the movement is the same as minimizing its root mean square or RMS value. The RMS acceleration over the course of a movement is often minimized in robotics (2), since it would obviously be undesirable when transporting a load such as a glass of water to accelerate and decelerate too abruptly. Similarly, human movements are smooth, so it seems plausible that the jerkiness of a movement (jerk being defined technically in terms of the third derivative of position) might be minimized, and there is experimental support for this notion (15).

From Fig. 4A the measured wrist move-

ments agree reasonably well with the minimum acceleration predictions, but the sharp accelerations and decelerations predicted at the start and end of the movements do not occur. The minimum jerk predictions are clearly better, but there are still deviations from our measurements in regard to *I*) the timing and magnitude of the peak acceleration and deceleration, and *2*) the predicted symmetry between the acceleration and deceleration phases of the movement.

For example, the peak acceleration and peak deceleration in a minimum jerk movement should occur at $t = t_0 + 0.21 T$ and $t_0 + 0.79 T$. At these peaks jerk will be zero, so these values can be readily obtained by differentiating Eq. 3 three times and setting the result equal to zero. In fact, the peaks occur at times corresponding to $t_0 + 0.38 T$ and $t_0 + 0.52 T$ (i.e., at times much closer to the midpoint of the movement). Similar discrepancies were observed under a variety of conditions.

Since the minimum acceleration prediction is even worse (the peak accelerations should occur at the start and end of the movement), better agreement might be achieved by minimizing still higher order derivatives. The fourth derivative of position is referred to as "snap" and a similar calculation to that for jerk shows that the maximum acceleration and deceleration would occur under a minimum snap prediction at $t = t_0 + 0.28 T$ and $t_0 + 0.72 T$, values that are closer to, but still differ from, those observed experimentally.

Few people would argue seriously that the nervous system computes higher derivatives of position such as jerk or snap, much less that it squares the values and integrates them over the course of all possible movements to find the minimum jerk or minimum snap trajectory. Thus, even if a movement is well fitted with a minimum jerk prediction, the reason for this fit must still be determined.

One possible mechanism is that muscles and joints are well damped systems, so that even higher-order derivatives change smoothly and slowly and never have a chance to reach large values during the course of normal movements. Interestingly, the best fits to the minimum jerk prediction occurred with inertial loads (Fig. 8C). The impulse response of the system (see the AP-

pendix) the rivative term mass and of Therefore, if will change these conditions.

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Minimizing

Another c might be pla consumption PENDIX) then contains third (and fourth) derivative terms, which depend on the inertial mass and often dominate the solution. Therefore, it is inevitable that acceleration will change slowly and continuously under these conditions.

Put another way, inertial loads act as mechanical low-pass filters, so that higher-frequency components in EMG will not affect the movement. Although the minimum jerk predictions for acceleration are a cubic polynomial, the form is not very different from that of one cycle of a sine wave. Thus mechanical damping that reduces higher-order derivatives and hence high-frequency components may lead to a trajectory similar to the minimum jerk prediction. It was also pointed out in the RESULTS that previous experimental tests have been carried out under conditions where the inertial term is likely to have been dominant, so it is not surprising that a good agreement with the predicted minimum jerk trajectory was often found.

For elastic and viscous loads, better fits were generally obtained by assuming that the velocity followed a normal or Gaussian curve. According to the central limit theorem in statistics (3) the sum of a number of random variables with a given mean and standard deviation will be distributed according to a Gaussian curve. Thus Gaussian curves are seen frequently in a large number of systems where there are many stochastic elements, as is certainly true of the nervous system. However, the Gaussian curve is symmetric, as the minimum jerk prediction and the biexponential curve are. Deviations from symmetry have been observed under a wide range of conditions, even with inertial loads (11), and they appear more prominent with elastic and viscous loads. Such deviations can not be explained by recourse to minimization of the RMS value of higherorder derivatives. Under the assumption that the movement begins and ends at rest, the movement should always be symmetrical. The cause of the asymmetry will be considered further below under the heading of neural mechanisms.

Minimizing energy consumption

Another common idea is that movements might be planned so as to minimize energy consumption. Certainly, this is an appealing notion for stereotyped, repetitive motions such as running or walking over long distances. Also, in learning a skilled task extraneous muscle activity tends to drop out with practice so the task can then be continued for longer periods of time without fatigue. Whether these notions apply to the single joint movements, tested here over the course of one or at most a few sessions, is less clear.

The energy consumed by muscles is a complex quantity to estimate and will depend on the load against which the muscle is working. It requires a model of muscle such as one developed in (28) and further predictions from the model are considered in the APPENDIX. A number of interesting results emerge.

- 1) Equation A4 predicts for a purely elastic load that the energy consumption by the muscle will be minimized by moving at constant velocity, contrary to the observed trajectories against such loads. Thus these movements are clearly not carried out so as to minimize energy consumption.
- 2) Equation A5 predicts for a purely viscous load that energy will be minimized by a weighted sum of a constant velocity and a minimum acceleration trajectory, again contrary to observations.
- 3) Equation A6 predicts for a purely inertial load that energy will be minimized by a weighted sum of minimum velocity, acceleration, and jerk trajectories. Although the trajectories fitted the minimum jerk predictions quite well for an inertial load, we already discussed reasons for believing that this results from the damping of the mechanical system, rather than from any computation done by the central nervous system.

Finally, the form of the movement should clearly change when the nature of the load is changed from elastic to viscous to inertial, whereas it was relatively invariant (see also 24). Thus the results are either contrary to the predictions for minimizing energy consumption or not very convincing in their support of the predictions. If the simple model of muscle function, from which the predictions were derived in the APPENDIX, is satisfactory for this purpose, then we must conclude that the simple movements about one joint that were studied in this paper are not organized so as to minimize energy consumption.

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Neural mechanisms

The final possibility raised above was that the nervous system generated the movement by combining simple waveforms that could be produced in various motor centers of the brain. For example, saccadic eye movements are produced by a discrete burst of activity followed by tonic activity sufficient to maintain the new position. The burst of activity accelerates the eye to a roughly constant velocity and the duration of the pulse determines the total distance that will be covered (22).

The EMG generating the limb movements against the elastic loads studied here appeared to rise smoothly in a ramplike fashion to a peak (see Fig. 9), rather than increasing abruptly in a stepwise fashion to a high level, that was then maintained for varying periods of time. The production of ramplike increases in activity does not impose a great "computing burden" on the nervous system, as a minimum jerk computation might. In producing the slow phase of nystagmus the eye muscles also generate ramplike length changes through steadily increasing EMG activity.

After the peak the EMG often declined to the steady level needed to maintain the final position (Fig. 9). Again, no special neural mechanisms need to be postulated as the firing rate of motoneurons adapts with one or more exponentials to a steady level when constant currents are applied intracellularly and exponentially changing responses are found widely in the nervous system. The movement could be well predicted from the EMG (Fig. 10) within the limits imposed by the simple, linear, second-order muscle model used. These were the only predictions that accurately fitted the timing, amplitude, and asymmetry of the acceleration and deceleration peaks, although the variability of the EMG traces could increase the value for the RMS error in the position trace above those obtained with some of the smooth curves that were tested.

Not all the variability was purely random. The oscillations seen in Fig. 10 had frequency components near 10 Hz that were probably associated with physiological tremor. They were also more prominent at the end of the movement, when more force was being generated, than at the beginning,

another feature of tremor. Finally, the oscillations associated with the EMG at the two sites was often out of phase so that the resultant movement would be smoother than predicted from either EMG alone.

In conclusion, the data suggest that the nervous system does not plan the trajectory of the simple wrist movements studied here so as to minimize some complex quantity such as jerk or energy consumption. Rather. it combines a few basic functions that can be readily produced, probably by trial and error from the visual and kinesthetic feedback of the resulting movements, until a combination is found that produces approximately the desired movement in approximately the desired time. The damping in the muscles and joints produces a smooth movement that may under some circumstances approach that expected if jerk or some higher order kinematic parameter were being minimized over the course of the movement. This is a nice example of how muscle properties may automatically simplify the job of the nervous system in achieving a particular objective, namely a smooth movement to a target.

APPENDIX

A commonly used, linearized second-order model of muscle contains parallel and internal series elastic elements of stiffness K_p and K_i , a viscosity of magnitude B and an active force-generating component that decays exponentially with a rate constant β following a nerve impulse (1). If such a muscle is connected to a generalized load with an external spring of stiffness K_e , a viscosity of magnitude D and a mass M, the change in position in response to a nerve impulse is given by (1)

$$c_1 x''' + c_2 x'' + c_3 x' + c_4 x = g(t)$$
 (A1)

where $c_1 = MB/K_i$, $c_2 = [M(K_i + K_p) + DB]/K_i$, $c_3 = [D(K_i + K_p) + B(K_i + K_e)]/K_i$, $c_4 = [K_p(K_i + K_e) + K_iK_e]/K_i$ and $g(t) = c_5e^{-\beta t}$. c_5 is a constant that depends on the force generated by the muscle to an impulse input, and the symbol ' is used to indicate differentiation with respect to time. For a purely elastic load (M = D = 0), $c_1 = c_2 = 0$ and $Eq.\ AI$ simplifies to a first-order differential equation. For an arbitrary pattern of neural input n(t), which was estimated in this paper from the surface EMG, under the assumption that the form of g(t) remains the simple exponential given above, then it follows that

$$n(t) = \beta g(t) + g'(t) = mx'' + dx' + kx$$
 (A2)

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- 1. BAWA, P., tions and e model usir 22: 139-14
- 2. CHAUDET adaptive relation. In: edited by J sevier/Nor
- 3. Cox, D. R chastic Pro
- 4. DELONG, I functions *Physiology* Bethesda, sect. 1, cha

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where $m = c_3$, $d = \beta c_3 + c_4$, $k = \beta c_4$. Note that this equation is of the same form as that used to determine the effective load $(Eq.\ I)$. However, we have used lower case rather than upper case letters, since the parameters are not the usual mechanical parameters of the external mass, dashpot and spring, but depend on both the parameters of the load and the internal parameters of the muscle. In fact, $Eq.\ A2$ was derived under the specific assumption that the mass and viscosity were 0. A similar derivation can be made if D > 0 or M > 0. The resulting equation corresponding to A2 will have third and fourth differentials of position, respectively.

For the second-order model of muscle described above, minimization of energy consumption depends on minimizing an integral J_2 given by (Eq. 29 in Ref. 28)

$$J_2 = \int_0^T g(t)[g(t) - f(t)]dt$$
 (A3)

where g(t) is given by Eq. AI and f(t) is force as a function of time. It was also assumed in deriving Eq. A3 that the parallel elastic elements of muscle have a stiffness (K_p) that is small compared with that of the internal series elements (K_i) . This assumption is generally true for a contracting muscle.

For a pure spring load K_e (M = D = 0 and hence $c_1 = c_2 = 0$ and $c_4 = K_e$), Eq. A3 reduces to

$$J_2 = c_3^2 \int_0^T (x')^2 dt$$
 (A4)

Thus minimization of energy consumption by a spring load requires minimization of velocity squared over the course of the movement. It can easily be shown (28) that this will be achieved by a movement at constant velocity v = X/T.

For a purely viscous load D ($M = K_e = 0$ and hence $c_1 = c_4 = 0$), Eq. A3 reduces, after some manipulation, to

REFERENCES

- BAWA, P., MANNARD, A., AND STEIN, R. B. Predictions and experimental tests of a visco-elastic muscle model using elastic and inertial loads. *Biol. Cybern.* 22: 139–149, 1976.
- CHAUDET, J. AND O'SHEA, J. Validation of an adaptive robot control structure by means of simulation. In: Simulation in Engineering Sciences, edited by J. Burger and Y. Yarny. Amsterdam: Elsevier/North-Holland, 1983, p. 411-416.
- 3. COX, D. R. AND MILLER, H. D. *The Theory of Sto-chastic Processes*. London: Methuen, 1965.
- 4. DELONG, M. R. AND GEORGOPOULOS, A. P. Motor functions of the basal ganglia. In: *Handbook of Physiology. The Nervous System. Motor Control.* Bethesda, MD: Am. Physiol. Soc., 1981, vol. II., sect. 1, chapt. 21, p. 1017–1061.

$$J_2 = c_2^2 \int_0^T (x'')^2 dt + c_3^2 \int_0^T (x')^2 dt$$
 (A5)

Thus minimization of energy for a viscous load involves a weighted sum of the minimum (i.e., constant) velocity and minimum acceleration predictions.

Finally, for a purely inertial load $M(D = K_e = 0)$ and hence $c_4 = 0$), Eq. A3 reduces, after several intermediate steps that have been omitted here, to

$$J_2 = c_1^2 \int_0^T (x''')^2 dt - 2c_1 c_3 \int_0^T (x'')^2 dt + c_3^2 \int_0^T (x')^2 dt \quad (A6)$$

Thus minimization of energy for an inertial load involves a weighted sum of the minimum velocity, acceleration, and jerk predictions. These various predictions are considered in the DISCUSSION section on minimization of energy.

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- DELONG, M. R. AND STRICK, P. L. Relation of basal ganglia, cerebellum and motor cortex units to ramp and ballistic limb movements. *Brain Res.* 71: 327–335, 1974.
- 6. FLASH, T. AND HOGAN, N. The coordination of arm movements: an experimentally confirmed mathematical model. *J. Neurosci.* 5: 1688-1703, 1985.
- 7. FUCHS, A. F. AND KANEKO, C. R. S. A brain stem generator for saccadic eye movements. *Trends Neurosci.* 4: 283-286, 1981.
- 8. FUCHS, A. F. AND LUSCHEI, E. S. Firing patterns of abducens neurons of alert monkeys in relationship to horizontal eye movement. *J. Neurophysiol.* 33: 382–392, 1970.
- 9. GHEZ, C. Contributions of central programs to

- rapid limb movement in the cat. In: *Integration in the Nervous System.* edited by H. Asanuma and V. J. Wilson. Tokyo: Igaku Shoin, 1979, p. 305-320.
- GHEZ, C. AND VICARIO, D. The control of rapid limb movement in the cat. II. Scaling of isometric force adjustments. *Exp. Brain Res.* 33: 191–203, 1978.
- 11. GIELEN, C. C. A. M., VAN DEN OOSTEN, K., AND PULL TER GUNNE, F. Relation between EMG activation patterns and kinematic properties of aimed arm movements. *J. Mot. Behav.* 17: 421-442, 1985.
- 12. HALLETT, M., SHAHANI, B. T., AND YOUNG, R. R. EMG analysis of stereotyped voluntary movements in man. *J. Neurol. Neurosurg. Psychiatry* 38: 1154–1162, 1975.
- 13. HATZE, H. AND BUYS, J. D. Energy-optimal controls in the mammalian neuromuscular system. *Biol. Cybern.* 27: 9-20, 1977.
- HOGAN, N. An organizing principle for a class of voluntary movements. J. Neurosci. 4: 2745–2754, 1984.
- 15. HOGAN, N. AND FLASH, T. Moving gracefully: quantitative theories of motor coordination. *Trends Neurosci.* 10: 170-174, 1987.
- 16. KORNHUBER, H. H. Motor functions of cerebellum and basal ganglia: the cerebello-cortical saccadic (ballistic) clock, the cerebellonuclear hold regulator, and the basal ganglia ramp (voluntary speed smooth movement) generator. *Kybernetik* 8: 157–162, 1971.
- 17. LESTIENNE, F. Effects of inertial load and velocity on the braking process of voluntary limb movements. *Exp. Brain Res.* 35: 407–418, 1979.
- 18. Mannard, A. and Stein, R. B. Determination of the frequency response of isometric soleus muscle in the cat using random nerve stimulation. *J. Physiol. Lond.* 229: 275–296, 1973.
- 19. MARSDEN, C. D., OBESO, J. A., AND ROTHWELL, J. C. The function of the antagonist muscle during

- fast limb movements in man. J. Physiol. Lond. 335: 1–13, 1983.
- MILNER, T. E. AND IJAZ, M. M. Kinematics of constrained movements. Soc. Neurosci. Abstr. 11: 73, 1985
- 21. OGUZTORELI, M. N. AND STEIN, R. B. Optimal control of antagonistic muscles. *Biol. Cybern.* 48: 91–99, 1983.
- 22. ROBINSON, D. A. The mechanics of human saccadic eye movement. J. Physiol. Lond. 174: 245-264, 1964.
- 23. ROBINSON, D. A. Oculomotor unit behavior in the monkey. *J. Neurophysiol.* 33: 393–404, 1970.
- 24. RUITENBEEK, J. C. Invariants in loaded goal directed movements. *Biol. Cybern.* 51: 11–20, 1984.
- 25. SHAPIRO, D. C. AND WALTER, C. B. An examination of rapid positioning movements with spatiotemporal constraints. *J. Mot. Behav.* 18: 373–395, 1986.
- SOECHTING, J. F. AND ROBERTS, W. J. Transfer characteristics between EMG activity and muscle tension under isometric conditions in man. J. Physiol. Paris, 70: 779-793, 1975.
- 27. SOKOLNIKOFF, I. S. AND REDHEFFER, R. M. Mathematics of Physics and Modern Engineering. New York: McGraw-Hill, 1958.
- 28. STEIN, R. B., OGUZTORELI, M. N., AND CAPADAY, C. What is optimized in muscular movements? In: *Human Muscle Power*, edited by N. L. Jones, N. McCartney, and A. J. McComas. Champaign, IL: Human Kinetics. 1986, p. 131–150.
- 29. STEIN, R. B., ROLF, R., AND CALANCIE, B. Improved methods for studying the mechanical properties of biological systems with random length changes. *Med. & Biol. Eng. & Comput.* 24: 292-300, 1986.
- 30. ZELAZNIK, H. N., SCHMIDT, R. A., AND GIELEN, S. C. A. M. Kinematic properties of rapid aimed hand movements. *J. Mot. Behav.* 18: 353-372, 1986.

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SUMMARY

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