Exp Brain Res (1990) 81:199–208

Experimental Brain Research

An identified model for human wrist movements

S.L. Lehman and B.M. Calhoun

Department of Physical Education and Bioengineering Graduate Group, 103 Harmon Gym, University of California, Berkeley, CA 94720, USA

Received June 7, 1989 / Accepted November 27, 1989

Summary. We have performed tests to find the mechanical properties of the hand and muscles driving wrist flexion and extension, and have identified parameters of a model. The hand acts as a nearly pure inertial load over most of its range of motion. It can be approximated as a rigid body rotating about a single axis. Viscosity of the wrist joint is negligible. Passive elastic torques are also small, except at extreme wrist angles. We measured torque as a function of wrist angle for maximum voluntary contractions, and angular velocity as a function of load. The torque/velocity curves for shortening muscles are well approximated by a Hill equation. To measure the "series elasticity" of the muscle equivalents, we imposed step changes in torque. The series stiffness is a monotonically increasing function of the preload, or "active state", in the Hill sense. We discuss the relationship of the measured parameters to properties of isolated muscles. To see the implications of the model structure for the "inverse problem" of identifying motor control signals, we simulated four models of different complexities, and found best fits to movement data, assuming simple pulse-shaped inputs. Inferred inputs depend strongly on model complexity. Finally, we compared the best fit control signals to recorded electromyograms.

Key words: Parameter identification – Voluntary movement – Human wrist

Introduction

The wrist is a popular system for the study of single-jointed limb motor control. Hand position is finely controlled, and the hand and muscles are accessible for measurement and perturbation. Electromyographic (EMG) responses to imposed torques (Calancie and Bawa 1985a; Jaeger et al. 1982), reflex stiffness and viscosity (Gielen and Houk 1984), and EMG patterns in voluntary movement (Sanes and Jennings 1984; Calancie and Bawa 1985b, Litvintsev and Seropyan 1977) have all been reported.

Most papers have analyzed wrist responses without explicit models, though some investigators (Stiles 1983, Lakie et al. 1984; Stein et al. 1988) have characterized the wrist as a second order system. Explicit models are necessary if movements are to be simulated, or if control patterns are to be inferred from recorded movements. The recorded movement may include position and its derivatives, and net torques. The best available measure of a "control pattern" is often the electromyogram. The inference step is, in effect, an inversion of the operator that takes control pattern to movement (e.g. the computation of Hannaford et al. 1985). We hypothesize that the inferred control pattern should depend strongly on the operator being inverted (the model).

We have identified parameters of a fourth order lumped-parameter model (Fig. 1) for studying wrist movements. Our model includes, first, the mechanical properties of the hand, the wrist joint, and the passive muscles.

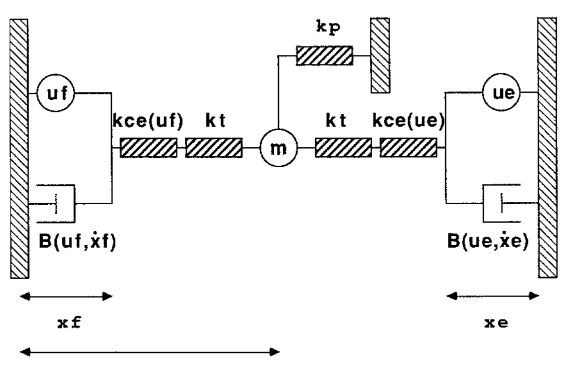

Fig. 1. The simplest model capable of the behaviors we measured includes an inertial mass m and a passive elastic element kp pulled by two muscle equivalents. Each "muscle" is composed of a force generator $u(t)$ in parallel with a velocity- and active state-dependent dashpot B (u, ẋ). These two are connected in series with two springs. One, kce (u) is active state-dependent, and the other, kt, has constant stiffness

Offprint requests to: S.L. Lehman (address see above)

Torques due to muscular activity are lumped into effects of two antagonistic "muscle equivalents". This lumping of forces produced by many muscles is justified, in part, by the fact that the relationship between torque and velocity, torque and angle, and series stiffness to preload are those one would expect from a single muscle. There is also some EMG evidence that all the wrist flexors turn on and off at the same time during rapid wrist movements (Litvintsev and Seropyan 1977).

We have not attempted to identify some properties. Activation and relaxation kinetics are the subject of a separate investigation. The inputs to our model are therefore the forces that the contractile element would develop, if the force/velocity curve played no part – Hill's "active state". Nor have we attempted to characterize a torque/velocity relationship for activated lengthening muscles.

Having identified parameters, we tested the model by simulating a fast wrist flexion. An optimization algorithm found the four-pulse input (two pulses per muscle equivalent) that minimized the difference between the simulated and actual wrist positions. We compare the derived "active state" pattern to electromyograms. Simulations of three simplified models test the hypothesis that inferred control pattern depends strongly on the complexity of the model.

Methods

Subjects

Subjects were three healthy adults between 21 and 40 years old. All protocols were approved by the Committee for the Protection of Human Subjects at the University of California, Berkeley.

Apparatus

The static parameter identifications were performed using a load cell (Sensotec Model 34) attached to a handle at one end and fixed to a table top by a large bolt at the other. Angles were varied in the static experiments by moving the bolt to one of several holes on a circle whose center was the hand (Fig. 2a).

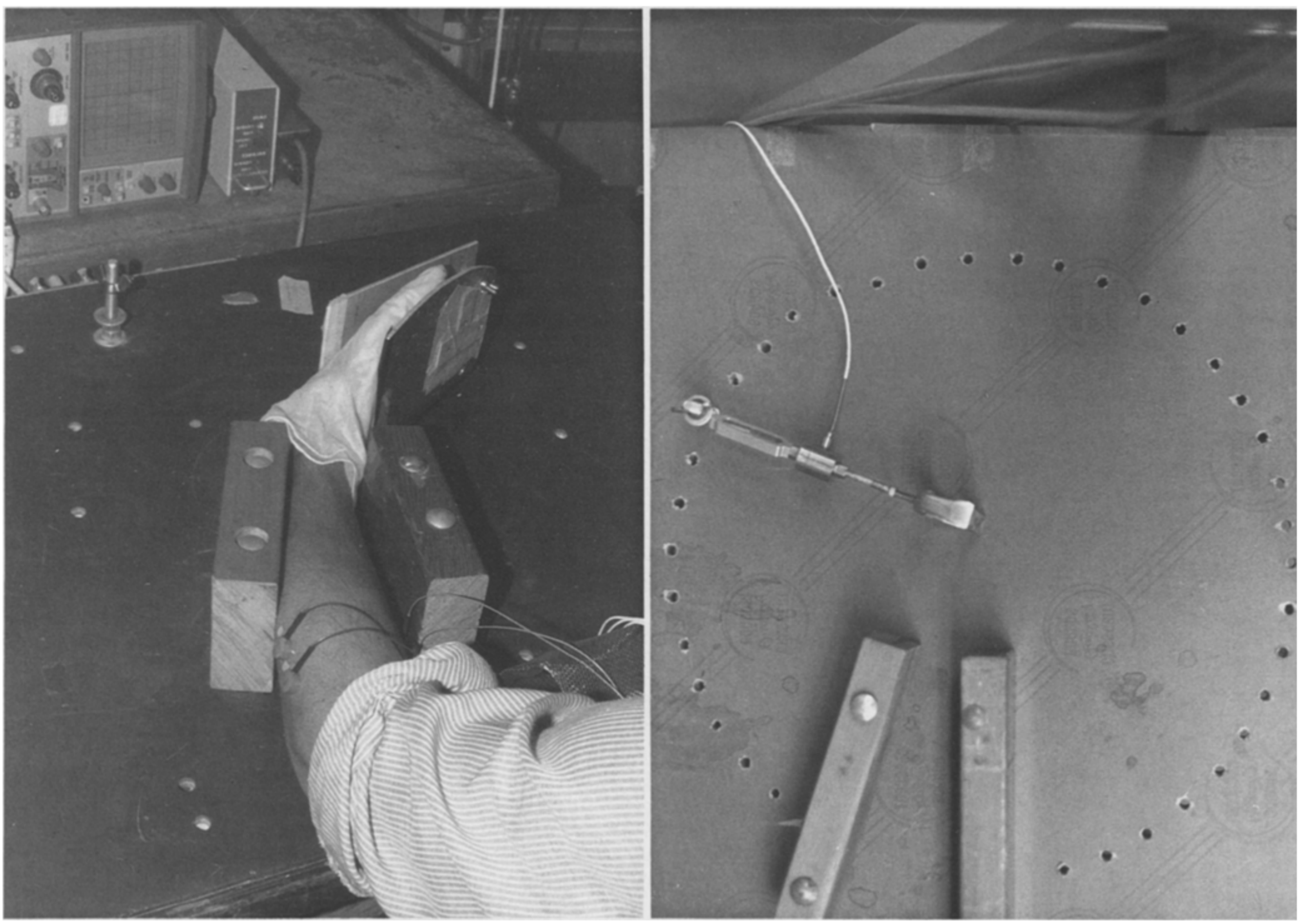

Fig. 2a, b. Apparatus used in the experiments. **a** Series stiffnesses, force/velocity characteristics, and voluntary movements were measured using a handle connected to a motor with position, torque and acceleration sensors. The computer-controlled motor produced constant torques and torque steps for the stiffness measurements. Constant torques for the torque/velocity determination were provided by hanging weights over a pulley at the edge of the table (not shown). Electromyograms (electrodes shown) were recorded in all experiments. **b** Passive and active torque as a function of angle were measured by with a force transducer connected to a handle, placed at many positions around a circle centered at the hand

The other parameter identifications and movement experiments were performed using a permanent magnet electric motor (Electrocraft Model 720), digitally controlled. The motor is mounted on the bottom of a small table, with the top of its shaft nearly flush with the table top (Fig. 2b). A rigid aluminum handle is mounted on top of the armature. The handle consists of a fixed plate and an adjustable one, between which the subject's hand is firmly held. The subject thus flexes and extends the open hand about the wrist axis, which is coincident with the motor axis. Wooden blocks on top of the table constrain the subject's forearm.

A potentiometer, an accelerometer and a torque transducer were fitted to the motor, and used to measure the movements. The motor has low inertia, but can produce a large torque (up to 6 Nm) and has a rapid response (mechanical time constant 4 ms). Driven by a power amplifier, it produces torque proportional to input voltage. We used this feature to produce step changes in torque to identify the series elastic elements.

For identification of the force/velocity characteristic, hanging weights were attached to the handle by a wire (bicycle brake cable) leading over a pulley at the edge of the table.

Electromyograms

Surface electromyograms were recorded during all of the tests. The electrodes were pairs of silver/silver chloride disks 8 mm in diameter, applied to the skin over the flexor carpi radialis and the extensor carpi radialis (Delagi and Perotto 1981), 2 cm apart. We checked for crosstalk by looking for activity in each channel during a maximum contraction of the opposite muscle group, and moved electrodes if significant crosstalk was found. Extraneous signals from finger flexors and extensors were eliminated by positioning – the hand was held flat by the handle, so that grasping was impossible. Signals were differentially amplified 2000–5000 times (Grass P511J), and bandpass filtered (half amplitudes at 10 Hz and 0.3 kHz). Sampling rate was 500 samples per second.

Results

Passive hand and wrist act as an inertia

The center of rotation of the wrist was found geometrically. The subject grasped a pencil and rotated the wrist through the full range of motion, with the forearm fixed on the table. Construction of the center by perpendicular bisectors of chords of this arc showed that the hand rotates about a single fixed center over most of the range of motion.

We measured the inertia of the apparatus by computing the acceleration imparted by a constant torque (0.375 Nm) applied by the motor. Digital differentiation of the position yielded a velocity, to which we fit a straight line by eye. The slope of this line gave acceleration. The inertia of the handle plus armature was 7.12×10^{-3} kgm^2. We also added known masses (500 g and 1 kg) to the handle at a fixed radius (0.1 m). Comparing the velocity for these known added inertias to that with the relaxed hand in the apparatus (Fig. 3), we found that the inertia of the 0.4 kg hand was 3.9×10^{-3} kgm^2. The measured inertia was close to that estimated from the hand mass, approximating the hand as a rigid parallelopiped, accelerated about one end (see discussion). Hand volumes were measured by water displacement, and masses estimated assuming a constant tissue density of 1 g/cm^3. Subject's hands varied in mass from 0.3 to 0.4 kg.

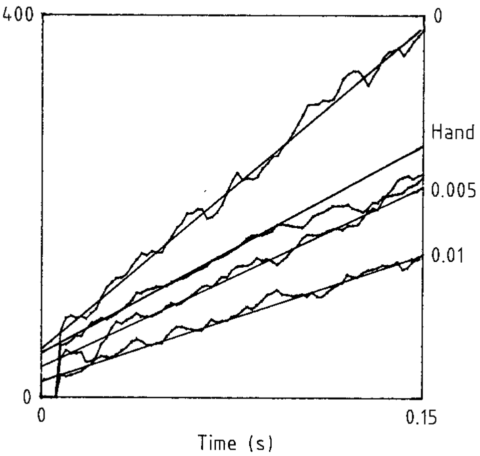

Fig. 3. Velocity vs. time for the motor connected to the handle and various loads (from top): handle alone, handle with relaxed hand, handle with 500 g mass 10 cm from axis, and handle with 1000 g mass 10 cm from axis. Up to about 0.1 s, the hand acts as a simple inertia

Velocity was linear (Fig. 3) up to approximately 100 ms (the latency of the myotatic reflex EMG is about 40–50 ms, and EMG to force production takes an additional 35 ms), so the passive hand could be viewed as a purely inertial load at the velocities measured.

Passive elastic torques are small over ±40 degrees

We measured the passive forces (produced by the relaxed hand) at intervals of 0.3 radian (17.5 degrees), over the full range of movement. The subject placed the knuckles against a handle attached through a load cell to a bolt, which was fixed to the table. The direction of pull was varied by moving the bolt to holes in the table top, equally spaced on a circle centered at the hand.

Passive torques were less than 0.1 Nm over the central 80 degrees of each subject's range of motion (Fig. 4). At either extreme of the range, torque rose rapidly.

Maximum torque is nearly independent of wrist angle over the same range

The maximum voluntary torque exerted by a subject was also nearly independent of angle over the central 80 degrees of the range of motion (Fig. 5), but declined sharply at each end of the range (to 20–25% of the maximum).

Torque-angular velocity relationships are well fit by Hill curves

We measured maximum velocity at a variety of fixed loads. The fixed torque was set by hanging a weight over the table edge, the weight attached to a cable which passed over a pulley to reach its attachment at the handle (ala Wilkie 1950). Subjects were instructed to move the

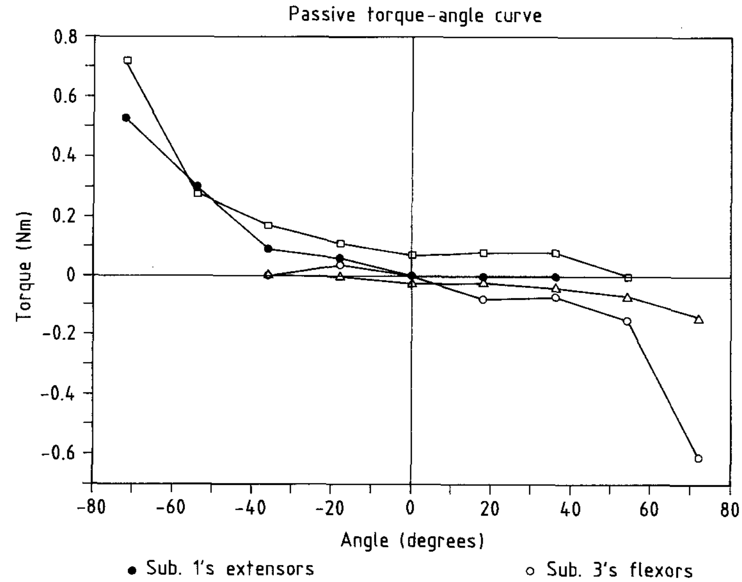

Fig. 4. Torque produced by relaxed hand as a function of angle for two subjects

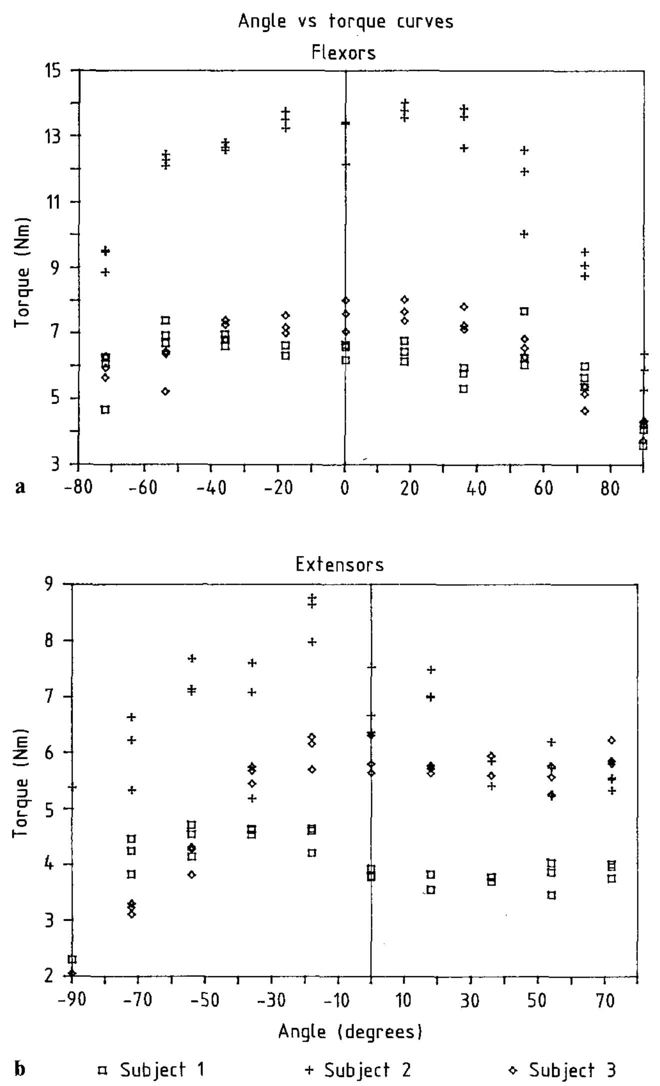

Fig. 5a, b. Maximum voluntary torque as a function of angle for three subjects' flexors (**a**) and extensors (**b**)

weight as fast as possible, and were told the peak velocity after each movement. Random ordering of the loads and ample rest periods between pulls reduced the likelihood of fatigue.

Wilkie (1950) noted that such a hanging weight apparatus produces both the constant torque due to the weight and a time-varying acceleration torque. His apparatus included a special lever system to minimize movement of the weight, and therefore the inertial torque. At the lightest loads, his subjects could not reach a maximum velocity (zero acceleration) within the range of motion. He therefore calculated (his appendix A) the theoretical velocity the arm would have reached, if it had no inertia, and scaled his velocity measurements accordingly.

Our subjects were able to reach and hold a maximum velocity before the end of the movement, even with the lightest loads. Perhaps the difference between wrist and forearm is due to the smaller inertia of the wrist, relative to the maximum torques produced by the muscles (Lehman and Stark 1983). In the worst case, the fastest movements, velocities peaked and stayed constant (to within 3%) for a period of 50 milliseconds. An accelerometer built into the apparatus verified that acceleration was indeed small during a time interval surrounding the time of peak velocity. During this peak, there was, of course, no acceleration and no inertial torque.

In our experiments, as in Wilkie's, the best argument for constant excitation during the movement is the consistent peak velocity we found at each load (Fig. 6). "The constancy of the mechanical response at all times makes it very likely that the excitation does remain constant, but a direct investigation has also been made by recording electromyograms during the movements" (Wilkie p. 272). Our electromyograms showed consistently high levels in the agonist around the time of maximum velocity, and minimal (relaxed) levels of electrical activity in the antagonist.

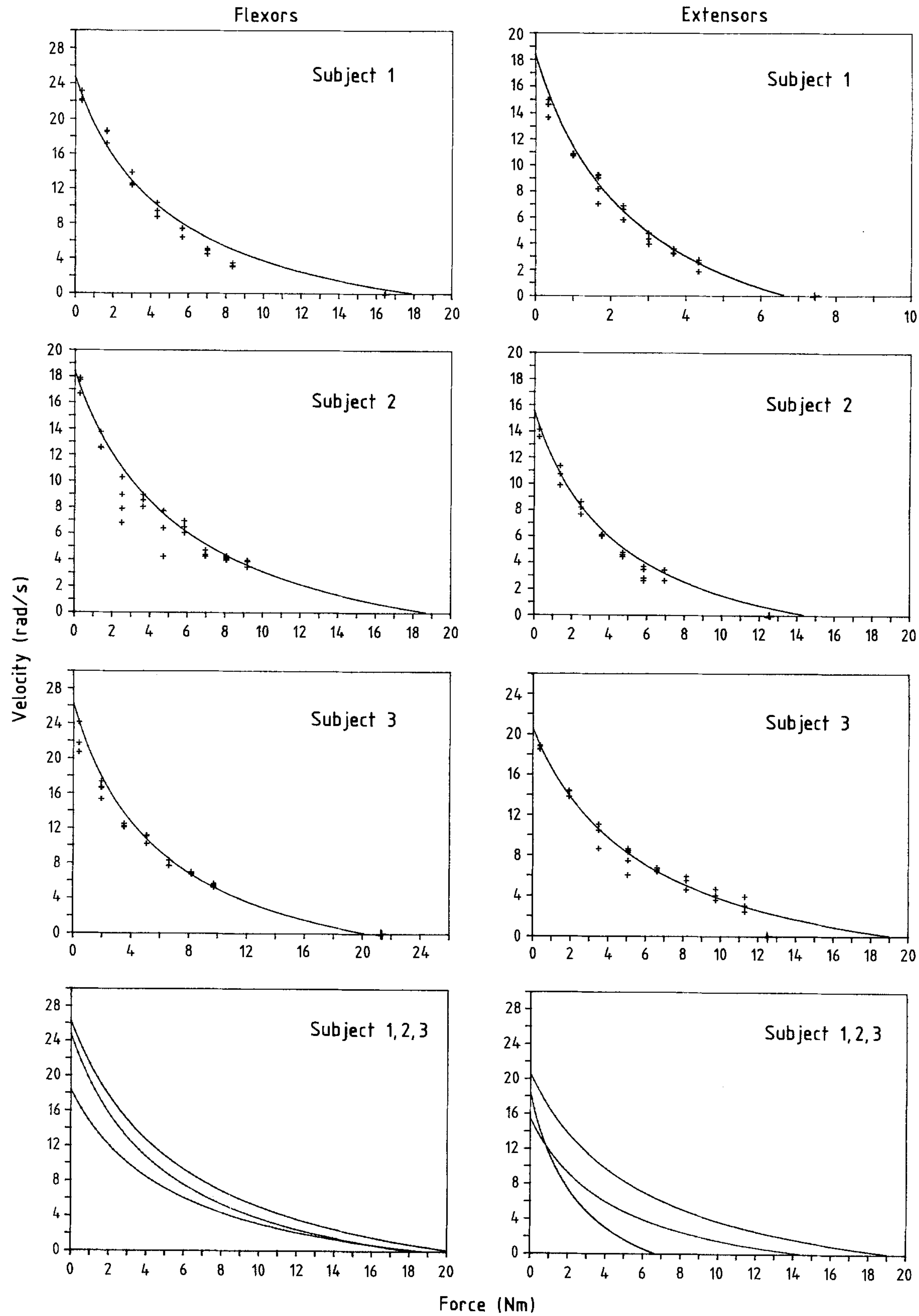

Fig. 6. Maximum voluntary angular velocity as a function of fixed torque for three subjects (top to bottom) – flexors (left column) and extensors (right column). Superimposed curves represent best-fit Hill hyperbolas. Summary curves (bottom) compare Hill fits for all subjects

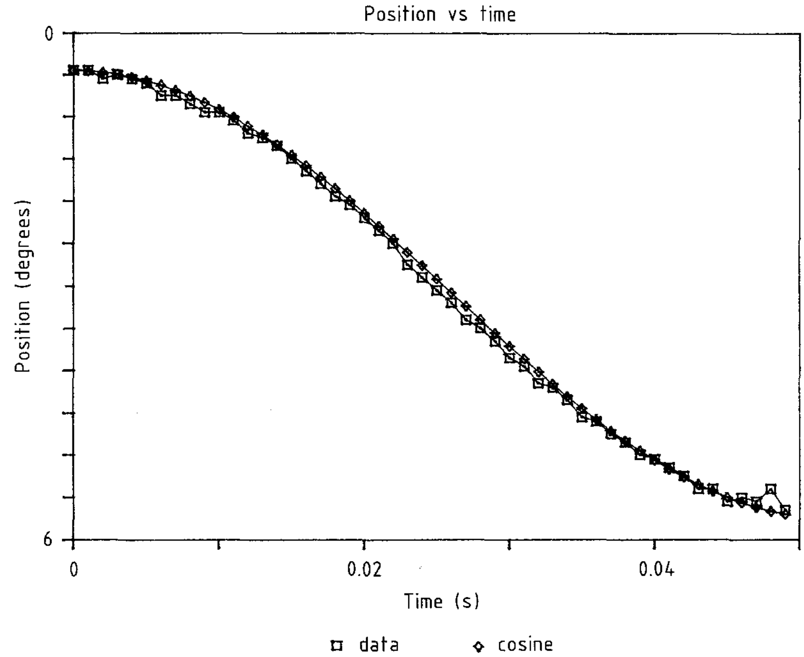

Fig. 7. Position (squares) as a function of time following a step decrease in torque applied to the hand. Overlaid diamonds show best fit cosine curve. Up to stretch reflex time, a spring and mass model the hand well

Isometric maximum torques varied between subjects, but were consistently about twice as large for flexors as for extensors (Fig. 5, 6). Given feedback, subjects were able to produce consistent maximum velocities at each load (Fig. 6).

The Hill force-velocity relationship:

$$(P+a)(V+b) = (P_0+a)\,b$$

was fit to each subject's data, varying P_0, V_{max} and a as free parameters. Least squares fits for each subject had errors of 1.1 to 5.9%, with a/P_0 between 0.28 and 0.41. V_{max} varied less than did P_0 between subjects, ranging from 15.3 to 26.2 radians per second.

Series elasticity –
preloaded wrist responds as a mass-spring

We measured the series elasticity of the muscle equivalents by a quick-release protocol (Jewell and Wilkie 1958). The subject first held a fixed position by producing a constant torque against the motor. The constant preload was intended to produce a constant "active state". The motor's torque was then stepped to a value 0.75 Nm lower than the preload. The experiment was repeated 6 times at each preload, at preloads varying from 0.75 to 6.0 Nm.

The response of an isolated muscle to a quick change in load is well known: a rapid change in length attributed to the series elastic element, followed by a slower component attributed to the interaction of the contractile element and the series elasticity. If the hand responded as a mass attached to a spring, the wrist angle would be

$$x(t) = (F/k)(1-\cos \omega t)$$

where F is the constant torque after the step, k the spring constant, $\omega = \sqrt{k/m}$. The wrist angle was well-approximated by a cosine over the first 40 ms (Fig. 7). We measured both the frequency of this cosine and the maximum excursion, and deduced the short-range stiffness. Plotting stiffness as a function of initial torque (Fig. 8) we found that the short-range stiffness was proportional to torque for small initial torques. The slope was about the same (0.9 to 1.8 rad^{-1}.) for each subject and for each muscle. Measurement errors became significant at the larger preloads (smaller deflections F/k).

Discussion

Passive properties

Over the middle of the range of motion (40 degrees either direction from the resting position) the hand acts as a nearly pure inertial load, moving about a single axis.

The inertia could well be estimated, approximating the hand as a rectangular parallelopiped of mass M and length a, rotated about one end. The parallel axis theorem then gives the inertia:

$$I = Ma^2/12 + M(a/2)^2 = Ma^2/3$$

For the subject whose hand was measured, the mass was 0.4 kg, the measured I was 3.9×10^{-3} kgm^2, so $a = 17$ cm. The length of this subject's hand was 18 cm.

That viscous and passive elastic torques are small is shown in the constant torque input experiment (Fig. 3), the cosine fit to the response to quick release (Fig. 7) and the direct passive stiffness measurement (Fig. 4).

The resonance data of Lakie, Walsh and Wright (1984) yields indirect, but fine estimates of these small

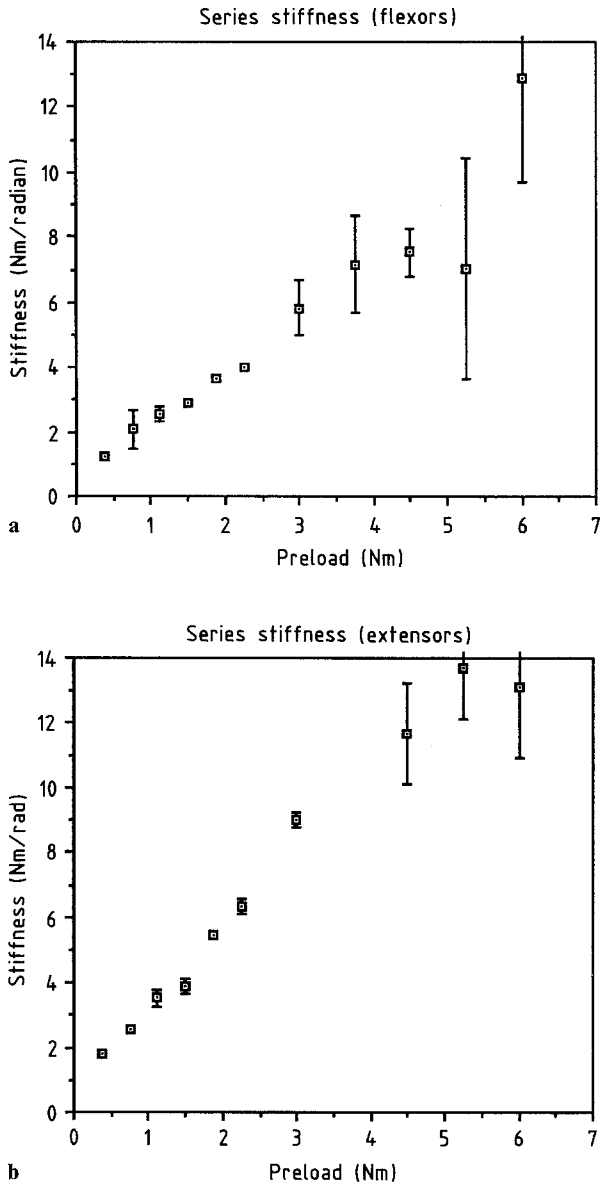

Fig. 8a, b. Stiffness as a function of preload (active state) for (**a**) flexors and (**b**) extensors of one subject

torques. They used rhythmic torque inputs of gradually increasing frequencies (chirps) to drive the relaxed wrist. They excited resonances at about 2 Hz, for a variety of subjects, whether awake or anaesthetized. Using our measured inertia, this resonant frequency corresponds to a stiffness of $\omega_x^2 I = 2 \times 10^{-3}$ Nm/radian. Lakie et al also measured a quality factor Q of 0.25. From this Q we deduce a damping factor $\gamma = \omega_0/Q = 8\ s^{-1}$, and a viscous coefficient $B = \gamma J = 4 \times 10^{-3}$ Nm/radian/s.

For small torques (small excursions) Lakie et al found resonant frequencies 4 times higher. These would imply a 16-fold greater stiffness and a 4-fold greater viscous coefficient.

For a movement starting at the middle of the range of motion and staying within the middle range (0.5 radian), the passive elastic torque would then be on the order of 10^{-3} Nm. P_0 for the wrist is on the order of 10 Nm, so the passive elastic torque is four orders of magnitude smaller. Elastic torques are therefore comparable to active state only during posture. In a very rapid movement, wrist velocity might reach 10 radians per second, so viscous torques would peak at around 10^{-1} Nm, or 1/100 of P_0. Joint viscosity is therefore never significant.

Active properties

The shape of the active torque vs. angle curve depends on the subject (Fig. 5), but maximum torque generally shows only a weak dependence on angle.

The equivalent flexor and extensor have torque/velocity curves like force-velocity characteristics of isolated muscles. This, and evidence that the muscles are turned on and off at the same time during a variety of movements (Litvintsev and Seropyan 1977), justify lumping the flexors and extensors into two single muscle equivalents.

Series elasticity

Our imposed step reductions in torque produced trajectories well-fit by cosine curves (Fig. 7), as would be the case if the inertia of the hand were attached to a simple spring.

The cosine fit is good over a surprisingly large angle, given that the short-range stiffness exists only over a few percent of the rest length of the muscle. We therefore estimated the relationship between angular change and muscle length change from the geometry of the wrist joint (Fig. 9a). Given the angle of wrist rotation θ, the radius from the center of rotation to the tendon insertion r, and the distance from the center of rotation to the carpal tunnel w, one can compute the length L of tendon from the carpal tunnels to the tendon insertion on the palm by the law of cosines. If the wrist angle changes by $\Delta\theta$, one can compute the corresponding change in length ΔL by a second application of the same law. Assuming that $\Delta\theta$ is small, the change in length turns out to be

$$\Delta L = wr\Delta\theta \sin\theta / L$$

From a dissection, we estimated w to be about 2 cm, and $r = 7$ cm. For small movements about resting position, θ is about 90 degrees, $\sin\theta \cong 1$, and $L \cong r$. Then

$$\Delta L / L \cong wr\Delta\theta / L^2 \cong w\Delta\theta / r,$$

so a 1% change in tendon length would correspond to an angular change of about 0.01 r/w radians, or about 2 degrees.

Cosine curves fit the position trajectories over a range of about 6 degrees, or a few percent change in muscle length (like isolated muscles, cf. Jewell and Wilkie 1958).

It is also possible to estimate the muscle forces from the torques measured at the hand using the geometry (Fig. 9b). Let F denote the force exerted by the muscle, and f the projection of that force normal to the palm.

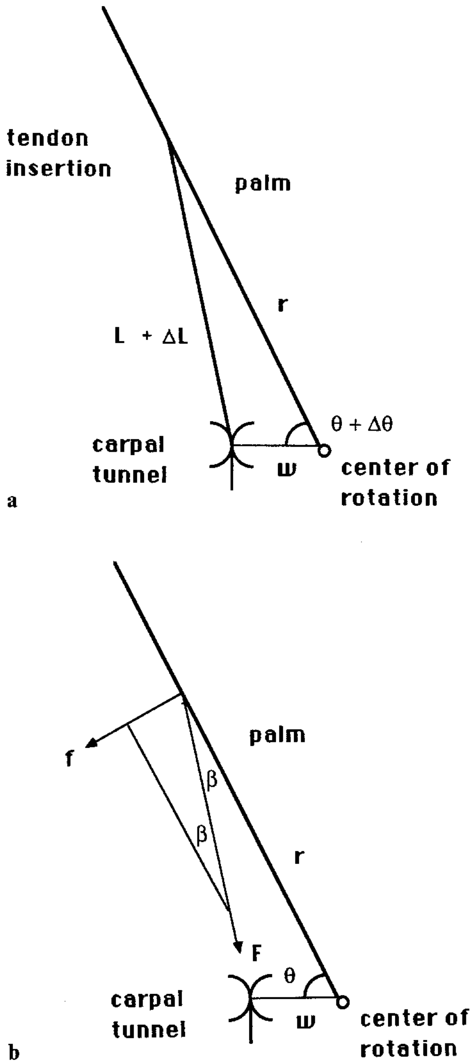

Fig. 9a, b. Geometry of wrist for comparison of (**a**) lengths and angles and (**b**) torque and force

Then

$f = F\sin\beta$,

and $\sin\beta/w = \sin\theta/L$ so $f = F(w\sin\theta/L)$

or $F=(T/r)\,(L/w\,\sin\theta)$ where T is the measured torque. Our maximum torques then correspond to muscle forces of about 1000 N and 500 N for lumped flexors and extensors, respectively.

From the length and force estimates, it is possible to derive an expression for muscle stiffness in terms of joint stiffness:

$$\Delta F/\Delta L = (L^2/w^2r^2\sin^2\theta)\Delta T/\Delta\theta.$$

Again with the hand in resting position,

$$\Delta F/\Delta L \cong (1/w^2)\Delta T/\Delta\theta$$

Our measured stiffness was up to about 18 Nm/rad (0.3 Nm/degree), corresponding to linear stiffness of about 5×10^4 N/m.

Isolated muscles have series elasticities composed of a tendon spring in series with an activation-dependent "cross bridge" spring. As the force rises, cross bridge elasticity becomes comparable to tendon elasticity, and series stiffness saturates (Morgan 1977). Our length measurements at high preloads were too noisy to allow us to determine whether stiffness saturated or not.

A rough estimate of tendon stiffness is possible. Young's modulus for tendon rises over the first few percent of strain, then levels off at about 10^9 N/m.^{2} (Wainwright et al. 1982, p. 89). To convert the Young's modulus of the tendon to stiffness requires estimates of the cross-sectional area and the length of the tendon. From dissection, the diameter of the flexor carpi radialis tendon is about 4 mm, and it is about 20 cm long. Its stiffness is then about $8\times10^4 \cong 10^5$ N/m.

Another way to estimate the tendon cross section is to use the fact that the maximum stress exerted on a tendon is between 1 and 2×10^7 N/m^2. If the muscle exerts 1000 N, it should then attach to a tendon with cross-sectional area between 0.5 and 1×10^{-4}m^2, i.e. a diameter of 4–8 mm. Such a tendon would have a stiffness of 0.8–1.6 $\times\,10^5$ N/m.

The largest stiffness we measured (at a preload of 6 Nm, or about 30% of P_0) was about half the estimated tendon stiffness.

Model simulation

To find the effects of the identified mechanical properties on a whole movement, and to see the influence of model complexity on inferred "active state" input, we simulated four models. The most complicated model was that shown in Fig. 1, where *M* is the inertia of the hand and handle, kce (*u*) and kt are series springs representing the crossbridge and tendon elasticities, B (u, $\dot{x}$i) is a variable dashpot to account for the force-velocity relationship and *uf* and *ue* are the "active state" of each muscle, in Hill's (Hill 1938) sense. The identified torque/angle relationships were not included in the simulations, because their effects are small over the range of interest.

The partition of the series elasticity into tendon (kt) and cross-bridge (kce) components followed from the identification of the series elasiticity from torque steps (Fig. 8). The tendon-like kt has the high constant stiffness we found at high active state. The elasticity kce was made proportional to active state in the model. The two elements were then combined in the model as series springs (that is, with compliances adding).

The torque/velocity characteristics were measured only for maximum "active state". In the models, we assumed that the given fractional active state scaled the force available from the muscle at each velocity in the same way. That is, the torque/velocity curve for half maximal active state has the same V_{max}, half the P_0 and half the torque at each velocity.

The approximations to the full identified model, in decreasing order of complexity, were: a fourth order Hill model in which the entire series elasticity was assumed to reside in the tendon, a linear fourth order model in

Table 1. Parameters used in simulations

Param.	value	Units	Remarks	Used in model
m	3.9×10^{-3}	Kg m^2	Inertia of hand	I, II, III, IV
M	7.12×10^{-3}	Kg m^2	Inertia of apparatus	I, II, III, IV
P_{0f}	21.0	Nm	Max torque, flexors	I, II, III, IV
P_{0e}	12.5	Nm	Max torque, extensors	I, II, III, IV
D_0	0.035	s	EMG to movement delay	I, II, III, IV
V_{max}	20.0	rad/s	Max shortening velocity	II, III, IV
kt	10.0	Nm/rad	Tendon stiffness	II, III, IV
a/P_0	0.25		Hill a	III, IV
kce	1.5	1/rad	CE stiffness per unit a.s.	IV

which the viscosities B were assumed constant, and a second order model consisting only of the inertia. Parameters for all the models are listed in Table 1.

We simulated each model in C on an IBM PC/AT. In each case, we allowed square-wave inputs, with two pulses each of agonist and antagonist "active state". The height of each pulse, its width, and the delay before the pulse were free parameters (12 in all). We used an optimization algorithm to minimize root mean square error between model wrist position and a typical wrist movement trajectory, varying the input pattern.

The prototype wrist trajectory is a voluntary flexion of 0.23 radians (13 degrees), made as fast as possible, and measured using the motor apparatus already described (Fig. 2b). One of our three identified subjects placed his hand in the handle and viewed a target consisting of two lines on an oscilloscope (Fig. 2). By flexing and extending the wrist, he moved a cursor across the screen, into the target area (10% of movement amplitude wide). After a random delay of 0–4 s, the target jumped 13 degrees. The subject was instructed to move as rapidly as possible to the target, as soon as it jumped. After practicing for 20 to 30 trials, all subjects were able to make consistent movements (maximum standard deviation less than 10% of the movement amplitude), with consistent EMG bursts. The EMG's in Fig. 10 are rectified records from the single movement shown.

Simulation results

Good fits for all the models required the active state be delayed from EMG onset. In each case, the delay was around 35 ms. This delay includes the time from de-

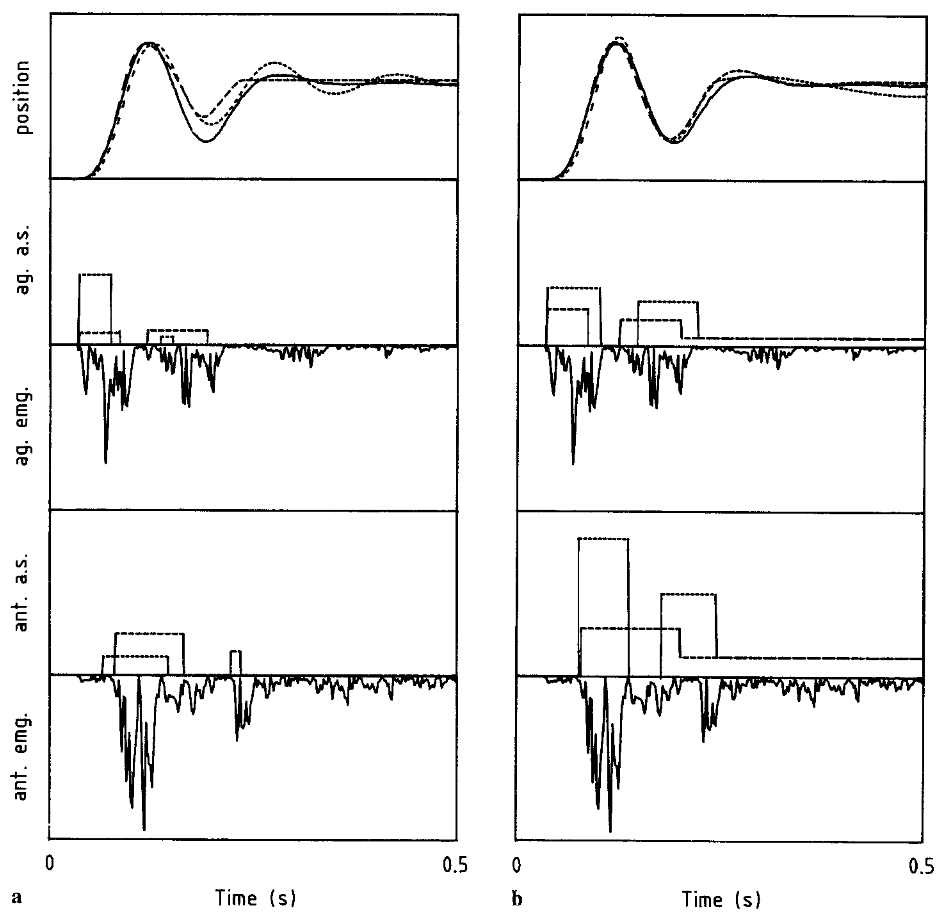

Fig. 10. a Linear models compared to a wrist movement. From the top, wrist angle best-fit agonist pulses, rectified flexor EMG (inverted for visual comparison), best-fit antagonist pulses, and rectified extensor EMG for a single fast wrist flexion. Long dashes denote a second order model (inertia alone). Short dashes correspond to fourth order linear model. **b** Hill model (long dashes) and full identified model (short dashes) compared to a wrist movement. Same axes as in **a** for the model with Hill force-velocity curves and constant series elasticities, and the full model, with partitioned series elasticity

polarization of the sarcolemma to force production, so part is true delay and part is the complicated kinetics of excitation-contraction coupling.

For each model, it was possible to tune agonist and antagonist active state pulses so that the model position matched actual position fairly well (rms errors $< 10\%$ full range, see Fig. 10). However, the deduced active states were very different from each other.

For the model consisting of the inertia alone (Fig. 10a, long dashes), driven by the difference between agonist and antagonist torque, the best-fit input approximated the acceleration (the hand is well-approximated by an inertia).

The linear fourth order model (Fig. 10a, short dashes), has constant series stiffness and muscle viscosity. The series springs and mass constitute a resonant system whose ringing, damped by the dashpot, can be driven to fit the wrist position. Late in the movement especially, the resonance of this system, and not the "active state" forcing, account for the shape of the trajectory. Note the vanishingly short (15 ms) second agonist pulse, and the absence of late antagonist pulse.

For the Hill model (Fig. 10b, long dashes), "viscosities" depended on shortening velocity and on "active state". For the model inversion, the dependence on active state is especially important. At low active state, the viscosities are small. The series springs and mass are therefore uncoupled from the force generator (Fig. 1), so the trajectory depends more on the forcing, and less on the mechanical resonance. For example (Fig. 10b), uncoupling means the second agonist burst must be longer to drive position to the final value after the undershoot. A sustained antagonist pulse overlapping the two agonist pulses does allow the springs to fit part of the trajectory.

When the series elasticity is in part active state dependent, the inertia is further uncoupled from the muscles at low force levels. Now (Fig. 10b, short dashes), the late trajectory is almost entirely governed by the forcing functions. The best-fit active state has two agonist pulses, now separated by a longer delay than for the other models, and a sizable second antagonist pulse. For this model, the widths of the four pulses are approximately equal, as are the pulse widths of EMG.

Thus the inferred "active state" depends strongly on the assumed model, and the measured EMG and the forcing functions correspond more closely for the fullest model. The activation-dependent elasticities we measured show large effects on the inferred forcing function late in the movement, when activation is small.

References

Calancie B, Bawa P (1985a) Firing patterns of human flexor carpi radialis motor units during the stretch reflex. J Neurophysiol 53:1179–1193

Calancie B, Bawa P (1985b) Voluntary and reflexive recruitment of flexor carpi radialis motor units in humans. J Neurophysiol 53:1194–1200

Delagi EF, Perotto A (1981) Anatomic quide for the electromyographer. Charles C Thomas, Springfield, IL

Gielen S, Houk J (1984) Nonlinear viscosity of the human wrist. J Neurophysiol 52:553–569

Hannaford B, Kim WS, Stark L (1985) Inverse modeling to obtain head movement controller signals. Proc Ann Conf on Manual Control

Hill AV (1938) The heat of shortening and the dynamic constants of muscle. Proc R Soc B 126:136–195

Jaeger, RL, Gottlieb, GL, Agarwal, GC (1982) Myoelectric responses at flexors and extensors of the human wrist to step torque perturbations. J Neurophysiol 48:388–402

Jewell, Wilkie DR (1958) An analysis of the mechanical components in frog's striated muscle. J Physiol 143:515–540

Lakie M, Walsh EG, Wright GW (1984) Resonance at the wrist demonstrated by the use of a torque motor: an instrumental analysis of muscle tone in man. J Physiol (Lond) 353:265–285

Lehman SL, Stark LW (1983) Perturbation analysis applied to eye, head, and arm movement models. IEEE Trans Systems, Man and Cybern SMC-13:972–979

Litvintsev, Seropyan (1977) Muscular control of movements with one degree of freedom. Avtomatika i Telemekhanika 5:88–102

Morgan DL (1977) Separation of active and passive components of short-range stiffness of muscle. Am J Physiol 232:645–649

Sanes J, Jennings, (1984) Centrally programmed patterns of muscle activity in voluntary motor behavior of humans. Exp Brain Res 54:23–32

Stein RB, Cody FWJ, Capaday C (1988) The trajectory of human wrist movements. J Neurophysiol 59:1814–1830

Stiles RN (1983) Lightly damped hand oscillations: acceleration-related feedback and system damping. J Neurophysiol 50:327–343

Wainwright SA, Biggs WD, Currey JD, Gosline JM (1982) Mechanical design in organisms. Princeton University Press, Princeton, p 89

Wilkie DR (1950) The relation between force and velocity in human muscle. J Physiol 110:249–280