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Systematic nonlinear relations between displacement amplitude and joint mechanics at the human wrist

Mark Halaki [a], Nicholas O'Dwyer [a,*] and Ian Cathers [b]

[a] School of Exercise and Sport Science, The University of Sydney, Australia

[b] School of Biomedical Sciences, The University of Sydney, Australia

* Corresponding author: School of Exercise and Sport Science, University of Sydney, PO Box 170, Lidcombe NSW 1825, Australia. Tel.: +61-2-9351-9886; Fax: 61-2-9351-9204 E-mail: n.odwyer@usyd.edu.au.

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Abstract

This study quantified the systematic effects on wrist joint mechanics of changes in amplitude of displacement ranging from within the region of short range stiffness (0.2% of resting muscle length) up to 3% of resting muscle length. The joint mechanics were modelled using a second order system from which estimates of joint stiffness, viscosity, inertia, natural resonant frequency and damping ratio were obtained. With increasing amplitude of displacement, the stiffness decreased by 31%, the viscosity decreased by 73%, the damping ratio decreased by 71% and the resonant frequency decreased from 10.5 Hz to 7.3 Hz. The patterns of change in joint mechanics with displacement amplitude were nonlinear but systematic and were well described by power relationships with high R^2 values. These relationships provide normative data for the adult population and may be used in the modelling of human movement, in the study of neurological disorders and in robotics where human movement is simulated. The observed patterns of high initial stiffness and viscosity, decreasing progressively as displacement amplitude increases, may provide a good compromise between postural stability and liveliness of voluntary movement.

1. Introduction

The mechanical properties of joints play a crucial role in the control of movement both by influencing the amount of muscle force required to move a limb and by determining the reaction forces to perturbations of limb position and trajectory. It is well established that the amplitude of limb displacement has an important effect on joint mechanics. The intrinsic muscle structures (without stretch reflex input) exhibit high initial ‘short range stiffness’ for increases in length up to approximately 1% of the resting muscle length. This is followed by a sudden yield, after which the muscle stiffness remains constant at a lower level (Rack and Westbury, 1974). Studies of intact joint mechanics (with stretch reflex input) have reported that stiffness decreases as displacement amplitude increases, both in humans (Kearney and Hunter, 1982; Milner and Cloutier, 1998; Sinkjaer et al, 1988) and decerebrate cats (Nichols, 1985). Kearney and Hunter (1982) found a decrease in the stiffness of the ankle with increasing displacement up to 14° peak to peak amplitude, while Sinkjaer et al (1988) found that ankle stiffness decreased only between 1° and 2° of displacement and did not change from 2° to 7°. Some of the above studies reported that joint viscosity also decreases with displacement amplitude, although Kirsch et al (1994) reported no change in viscosity in decerebrate cats.

The pattern of decrease of both stiffness and viscosity with increasing displacement amplitude has been found to be nonlinear, with an initial steep decrease followed by a slower rate of change (Kearney and Hunter, 1982; Sinkjaer et al, 1988). The ankle was studied in both instances and the pattern was found to be consistent in five subjects by Kearney and Hunter (Kearney and Hunter, 1982) but less consistent in three subjects studied by Sinkjaer (Sinkjaer et al, 1988). Furthermore, the pattern was reported only descriptively and so has not been quantified. Such quantification would be useful in the modelling of human movement, in the study of neurological disorders of movement and in robotics where human movement is simulated. The purpose of the present study, therefore, was to quantify this relationship between amplitude of joint displacement and mechanics at the human wrist. To confirm the consistency of the pattern, a larger group of subjects was studied.

In previous studies of this topic, the amplitude of displacement was varied at fixed levels of joint torque (Kearney and Hunter, 1982; Sinkjaer et al, 1988). In monitoring joint torque, however, the level of co-contraction of muscles operating across the joint was not controlled and could have varied with displacement amplitude. Co-contraction is a strategy utilised to increase joint stiffness (De Serres and Milner, 1991; Milner et al, 1995) and to a lesser degree, damping (Milner and Cloutier, 1998). Hence, unobserved changes in muscle co-contraction could have influenced joint mechanics in these previous studies. In the present study, therefore, we monitored wrist flexor and extensor EMG activity and controlled the level of contraction of the wrist flexor as the amplitude of wrist displacement was varied.

2. Methods

2.1 Subjects

Ten subjects, five males and five females, with a mean age of 35 years (range 26-50 years) and no history of musculoskeletal or neurological diseases, volunteered to participate in this study. The University of Sydney Human Ethics Committee approved the experimental procedures. Subjects gave their written informed consent prior to testing.

2.2 Equipment

Subjects were seated with the shoulder abducted at approximately 60°, the elbow flexed at 30° from full extension, the forearm supinated and the palm facing medially. The forearm was firmly strapped into a manipulandum which allowed rotation of the wrist (Figure 1). The wrist was positioned directly above the rotational axis of the manipulandum. The hand was then firmly clamped at the distal metacarpals in a padded ‘U’ bracket attached to the manipulandum. The bony location chosen for the clamp and the tightness of the clamp ensured that the connection was stiff but not so tight as to induce ischemia. To minimise movement of the fingers, they were taped together in a flexed posture.

Insert Figure 1 here

The manipulandum was fixed to the shaft of a DC servomotor (Baldor, ASR Servotron SD55-15-AI) which provided a peak torque of 16 Nm and was driven by a servo-controller (Baldor, UM4-150-2-045) configured to run in position control mode. The reference signal was provided from a computer-driven digital to analog card and a rotary variable differential transformer (Sakae, KSM-2201) fixed to the shaft of the servomotor provided position feedback. Motor torque was monitored using a torque transducer (Transducer Techniques, TRT-500) fixed in series between the motor shaft and the manipulandum.

Pairs of silver/silver chloride surface electrodes of 10 mm diameter with centres approximately 25 mm apart were applied to measure EMG signals from each subject. Two electrodes were attached above flexor carpi radialis (FCR), centred on the midpoint of a line from the lateral aspect of the biceps tendon at the elbow crease to the pisiform bone. Another pair was attached above extensor carpi radialis (ECR), centred one third of the distance along a line from the lateral end of the elbow crease to the middle of the wrist. This positioning of the electrodes allows maximal pick-up of signals from these muscles (Basmajian and Blumenstein, 1980). The earth electrode was fixed at the olecranon of the ulna. The EMG signals were amplified with a gain of 1000 and band-pass filtered (Biopac Systems, EMG100B) between 10 Hz and 5 kHz.

In order to monitor the contraction levels of other muscles acting at the joint, more extensive sampling of the muscles around the joint was carried out using intramuscular electrodes in one subject. Bipolar fine wire electrodes (221-24-730, Chalgren Enterprises Inc.) were employed. Each consisted of two strands of 0.05 mm insulated nickel alloy wire, stripped of 2 mm of insulation at each end and bent over at the protruding end of a 27 gauge 30 mm long hypodermic needle. In addition to flexor carpi radialis, the following prime flexor (Backdahl and Carlsoo, 1961) and extensor (McFarland et al, 1962) muscles were sampled: flexor carpi ulnaris (FCU), flexor digitorum superficialis (FDS), flexor digitorum profundus (FDP), extensor carpi radialis longus (ECRL), extensor carpi radialis brevis (ECRB), extensor carpi ulnaris (ECU) and extensor digitorum (ED).

The manipulandum angular displacement, torque and EMG signals were sampled at a rate of 2 kHz with a 16-bit analog to digital converter (Biopac Systems, MP100A) using proprietary data acquisition software (AcqKnowledge, Version 3.5.3).

2.3 Procedures

The right arm was tested in all cases. To control for diurnal variation, the sessions were conducted at a similar time of day. At the beginning of the session each subject was asked to relax completely and a baseline of EMG was recorded. They were then asked to produce maximum voluntary contractions (MVC) of FCR and ECR by flexing and then extending their wrist against the fixed manipulandum with the wrist in neutral position. Subjects were exhorted to make a maximal effort while feedback of contraction levels from the surface electrodes overlying FCR and ECR was provided. The contraction level display was generated by high pass filtering (10 Hz cut-off), rectifying and low pass filtering (0.5 Hz cut-off) the surface EMG signal and then subtracting the baseline EMG. The resultant signal was displayed as a trace on a computer monitor. Three measures of maximum contraction level were obtained at the beginning of each session, with a one-minute rest between each. The maximum for the three trials of the peak value reached by the rectified and filtered EMG was taken to be the MVC of each muscle. The peak was equivalent to the average level of the rectified EMG over a time window of 0.3 seconds.

For the data collection trials, subjects were instructed to flex the wrist against the manipulandum while maintaining a target contraction level in FCR of 15% of MVC. This produced a net flexor torque at the wrist. The contraction level was chosen to avoid fatigue while still providing a reasonable signal-to-noise ratio in the EMG signals. Feedback of contraction level was again provided on the computer monitor, scaled so that the target contraction level was shown as a horizontal line across the middle of the monitor, with 0% at the bottom. The duration of each trial was only 20 seconds and the subjects had no difficulty complying with the procedure, so it was anticipated that the contraction levels in all muscles would remain relatively constant throughout the trial. The more extensive muscle sampling in one subject was designed to test this assumption.

2.4 Displacement signals

Sinusoidal displacement signals with six different root mean square (RMS) amplitudes were employed: 0.4º, 0.5º, 0.6º, 2º, 4º, 6º RMS. In order to enable determination of wrist joint mechanics, 10 different frequencies from 3 Hz to 12 Hz in increments of 1 Hz were employed at each amplitude of displacement. Hence, with 10 frequencies and six amplitudes, there were a total of 60 displacement signals. Two broad bandwidth (3-12 Hz) displacement signals, with RMS amplitude matched to the 0.4º and 2º sinusoidal signals, were also tested. Whereas the sinusoids tested each frequency in separate trials, the broadband signals tested each frequency in the same trial and were employed to check the linearity of the mechanical frequency response. The disadvantage here was that a trial duration of 60 seconds was required with the broadband signals in order to provide a sufficient number of cycles at each frequency for adequate reliability of measurement.

Calculations using anatomical (Horii et al, 1993; Lieber et al, 1990) and physiological (Campbell and Lakie, 1998; Hill, 1968; Wiegner, 1987) data were carried out to determine the changes in muscle length that these signals would produce in FCR. These calculations indicated that the six displacement amplitudes corresponded to 0.2, 0.25, 0.3, 1, 2, and 3 percent of average muscle length. This indicates that the 0.4º, 0.5º, 0.6º RMS displacements were within the region of short range stiffness (< 1% of resting length (Rack and Westbury, 1974) for FCR, while the 2º, 4º and 6º RMS displacements were beyond that range.

Repeated measures analyses of variance (ANOVAs) were performed to determine the statistical significance of the experimental effects of the two factors of amplitude and frequency of displacement.

2.5 Signal analysis

Matlab (The Mathworks Inc., Version 6) was used for the data analysis. Since the frequencies of interest lie in the range below 15 Hz, the displacement and torque signals were low-pass filtered at 20 Hz (8^{th} order Butterworth). The EMG signals were first forward and reverse passed through a high-pass filter (8^{th} order Butterworth) with a 20 Hz cut-off frequency, in order to remove DC offsets and any low frequency movement artefact. The dual-pass process ensured that no phase changes were produced. The EMG signals were then full-wave rectified and low-pass filtered at 20 Hz (8^{th} order Butterworth). EMG signals processed in this way are henceforth referred to as IEMG (see Figure 3). The common low-pass filtering at 20 Hz precluded any change in the phase relation between displacement, torque and IEMG. The filtered signals were then re-sampled at 100 Hz. One second of data was truncated from the beginning of all trials to allow for final adjustments of contraction levels by the subjects.

The mechanical properties of the wrist were obtained using a cross-correlation and spectrographic analysis (Bendat and Piersol, 1971) to identify the best-fit linear relation between torque and displacement signals. This linear relation was described by gain, phase and coherence frequency functions. The gain of the mechanical response is defined as the amplitude of wrist displacement divided by the amplitude of wrist torque for each frequency and expressed in degrees/Nm. The phase of the mechanical response provided a measure (in degrees) of the relative time difference between the displacement signal and the torque signal at each frequency. The linearity and goodness of fit of the torque-displacement relation were quantified by the coherence square function.

The torque transducer provided a measure of the torque applied by the servomotor to the manipulandum. Therefore, by subtracting the torque due to the manipulandum alone from the total torque due to the manipulandum plus wrist, the mechanical contribution of the wrist alone could be determined. The linearity of these torque-displacement relations was confirmed by checking the coherence square between displacement and the torque due to the manipulandum alone (mean = 1.00, SD = 0.0002) and between displacement and the torque due to the manipulandum plus wrist (mean = 0.99, SD = 0.01). It was important also to ensure that the mechanical characteristics of the servomotor and manipulandum were linear across different amplitudes of displacement. This was confirmed by the fact that the gain and phase frequency response between displacement and the torque due to the manipulandum alone was close to identical for all amplitudes of displacement. Hence, any changes observed experimentally in the relationship between displacement and the torque due to the manipulandum plus wrist could be attributed to altered wrist mechanics and not to servomotor and manipulandum nonlinearities. Finally, the displacement signals were compared between trials of the manipulandum alone and trials of the manipulandum plus wrist (see Figure 3). The average coherence square between the signals was 1.00 (SD = 0.001), the average gain was 1.07 (SD = 0.08) degree/degree and the average phase was 3.20 (SD = 2.32) degrees, thus confirming that the kinematics were close to identical between conditions.

2.6 Modelling of the mechanical response

Several investigators have modelled the torque-angle relation of various human joints as a second order system and these models have generally provided an adequate description of the elastic stiffness, viscosity and inertia in response to various experimental conditions (Bennett et al, 1992; de Vlugt et al, 2001; Kearney et al, 1997; Lambertz et al, 2003; Perreault et al, 1998; Zhang and Rymer 1997). The mechanics of the wrist were also modelled as a second order mechanical system in the current study. The second order model can be expressed in the time domain as:

$$\tau(t) = I.d^2\phi(t)/dt^2 + B.d\phi(t)/dt + K.\phi(t)$$

where

τ = Torque (Nm)

ϕ = Joint angle (radians)

K = Torsional stiffness ($Nm.rad^{-1}$)

B = Torsional damping coefficient or viscosity ($Nm.s.rad^{-1}$)

I = Limb inertia = m r^2 ($kg.m^2$)

m = Mass of hand (kg)

r = Radius of gyration (m)

The transfer function between joint angle and torque is given by:

$$\frac{\phi(s)}{\tau(s)} = \frac{1}{I.s^2 + B.s + K}$$

where s is the Laplace transform.

For each subject, values of *I*, *B* and *K* were chosen to provide the best fit of the transfer function gain and phase versus frequency plots to the measured gain and phase of the wrist mechanical response. To achieve this, the RMS value of the differences between the modelled and measured gain and phase values of the mechanical response were calculated. Since gain and phase values are on different scales and have different offsets, the RMS differences between the modelled and measured gain and phase were each normalised to the respective average values across frequency of the measured gain and phase. Values of mechanical parameters (*I*, *B* and *K*) were iteratively changed to find the minimum average of the normalised differences between modelled and measured data. Different weightings on gain and phase were explored in this model fitting, from equal weighting on each to 100% weighting on either gain or phase (ie, using only the gain or only the phase values). The model fitting was found to be robust with respect to weighting scheme. When the values of the mechanical parameters derived using equal weighting were compared with those derived using only the gain or only the phase values, the average differences in the parameters were only 9% and 11% respectively. Hence, the equal weighting scheme was employed.

The goodness of the fit of the modelled data to the measured data, as indicated by the variance accounted for (VAF), is shown in Table 1. The VAF is described by the following equation:

$$\mathrm{VAF} = 1 - \frac{\mathrm{Variance}_{\mathrm{error}}}{\mathrm{Variance}_{\mathrm{measured}}}$$

It can be seen from Table 1 that the model had a good fit to the data in nearly every case, with an average VAF for gain of 0.88 and for phase of 0.98.

Insert Table 1 here

The fit of the model to the experimental gain and phase versus frequency functions is shown for two displacement amplitudes in one subject in Figure 2. The measured gain data in this subject at these amplitudes appeared to be somewhat noisy and these VAFs were the lowest observed in the study (subject 1 in Table 1). Nevertheless, the modelled curves still provided a reasonable representation of the measured data.

Insert Figure 2 here

2.7 Modelling of the mechanics versus displacement amplitude

The relations between changes in displacement amplitude and changes in mechanical variables (i.e. stiffness, viscosity, damping ratio and natural frequency) were modelled using linear regression analyses. In these analyses, the variability across subjects was effectively removed by setting the subject factor as random, i.e. using a linear model with a random intercept. Such a model also accounts for dependence across amplitudes for individual subjects, similar to the procedure employed in a one-way repeated measures analysis of variance, where the variability due to individual subjects is taken into account. Additionally, a simple interpretation of the slope can be given.

3. Results

3.1 Wrist torque and contraction levels

Typical torque, displacement and contraction level data are illustrated in Figure 3, which shows one second samples for the smallest and largest displacement amplitudes at 5 Hz. The reflex modulation of FCR is apparent but because the mean FCR contraction level was controlled by the subjects via feedback, it was kept very close to the 15%MVC target level (group mean = 14.8% ± 0.4%MVC). The level of activity in the ECR was low, so the net torque at the wrist was flexor in all trials. However, this flexor torque decreased by a small amount (from 1.5 ± 0.6 Nm to 1.0 ± 0.5 Nm) with increasing displacement amplitude ($F(5, 45)=19.68$, $p<0.001$). This decrease was due to small but systematic changes in the contraction levels of the other flexor and extensor muscles, for which no feedback or instructions were given regarding contraction level. Thus, the average contraction level of ECR increased across the six displacement amplitudes (see Figure 3) from 2.5%MVC at 0.4° RMS to 5.5%MVC at 6° RMS ($F(5, 45)=18.10$, $p<0.01$). The intramuscular EMG recordings in a single subject showed that the other unmonitored flexor and extensor muscles behaved similarly to the surface ECR recordings for the group. The contraction levels were low (mean levels across all amplitudes were FDP: 41 ± 10 μV; FDS: 38 ± 12 μV; FCU: 46 ± 6 μV; ECU: 33 ± 8 μV; ED: 55 ± 16 μV; ECRL: 61 ± 14 μV; ECRB: 32 ± 9 μV) and all increased by a small amount (mean = 27 ± 10 μV) from the smallest to the largest amplitude. By contrast, the average level of activity recorded intramuscularly in FCR was 101 ± 18 μV.

Insert Figure 3 here

3.2 Mechanics

The gain and phase of the mechanical responses of the wrist (i.e. between wrist torque and displacement) were consistent with those of a second order resonant system with stiffness, viscous and inertial components. The frequency of the peak in the gain curves corresponds to the system's damped resonant frequency while the frequency at which the phase crosses 90° corresponds to the undamped resonant frequency. Figure 4 shows the mean gain and phase between wrist torque and displacement for all amplitudes. Both the gain and phase lag of the mechanical response increased with increasing displacement amplitude ($F(5, 45) \geq 35.91$, $p<0.001$). The shape of the gain and phase curves also changed with increasing displacement amplitude, as shown by significant interactions between amplitude and frequency ($F(9, 81) \geq 13.57$, $p<0.001$).

Insert Figure 4 here

It can also be seen in Figure 4 that the gain and phase curves for the broad bandwidth displacement signals at 2° RMS amplitude closely matched the curves from the sinusoidal signals at this amplitude. A similar match between broadband and sinusoidal results was also found for the 0.4° RMS amplitude (not shown). This confirms the linearity of the mechanical frequency response and the validity of the second order model which was used to represent the wrist mechanics for all frequencies between 3-12 Hz.

Insert Table 2 here

The modelled values of inertia, stiffness, viscosity (damping coefficient), damping ratio and natural frequency for each subject are listed in Table 2. The group mean values of stiffness, viscosity, damping ratio and natural frequency for the six amplitudes of displacement are shown in Figure 5. The values for inertia did not change significantly with amplitude for the three smaller displacements nor for the three larger displacements ($F(2, 18) \leq 2.76$, $p > 0.09$). However, the inertia was larger for the three larger displacements than for the three smaller displacements ($F(1, 9) = 10.55$, $p < 0.05$). The stiffness, viscosity and damping ratio decreased significantly across all displacements ($F(5, 45) \geq 7.86$, $p < 0.001$). Post hoc tests showed that the changes were not significant for the smaller displacements ($F(2, 18) \leq 2.47$, $p > 0.11$) but were significant for the larger displacements ($F(2, 18) \geq 8.00$, $p < 0.05$). The natural frequency decreased with increasing amplitude for all displacements ($F(5, 45) \geq 66.04$, $p < 0.001$), including both smaller and larger displacements ($F(2, 18) \geq 9.01$, $p < 0.01$). It may be noted that the characteristics of the torque- displacement gain and phase versus frequency plots in Figure 4 (eg, the frequency of peak gain, the frequency where the phase lag crossed 90°, the shape of the gain and phase curves and the values of the DC gain as extrapolated from the curves) change with amplitude in a manner which is entirely consistent with these significant changes in the modelled mechanical parameters.

Insert Figure 5 here

The modelled values of *I* were compared to the values calculated from the anthropometric data of Winter (1990), where the mass of the hand was taken to be 0.61% of total body mass and the radius of gyration of the hand was taken to be 0.56 x hand length, as measured between the stylion and the head of metacarpal III. It can be seen from Table 2 that in every case except subject 2, who had the highest values of *I* in the group, the range of modelled values encompassed the value calculated using Winter's tables.

Since the plots in Figure 5 resemble power relations, log transforms of the data were carried out. Figure 6 shows the resulting linear relationships of the log of stiffness, viscosity, damping ratio and natural frequency versus the log of displacement amplitude for three typical subjects. These relationships could therefore be described by linear regression. Regression analyses for each subject revealed that, for every parameter, the slopes of all subjects were within two standard deviations of the mean of the group. As can be seen in Figure 6, however, the intercept was different for each subject. Therefore, for each of the mechanical parameters, all subjects were included in regression analyses with subject as a random factor (ie, with a random intercept) and slope set as a fixed factor. These regression analyses showed that the relationships between the four mechanical parameters and displacement amplitude were as follows:

$$MP = \beta A^{\alpha}$$

Where:

MP = Mechanical parameter

A = Displacement amplitude (°RMS)

β = Subject specific constant with means and ranges as indicated in Table 3

α = MP specific constant as indicated in Table 3

Insert Table 3 here

For illustrative purposes, the expanded model of the equation above for the mechanical parameter of stiffness (K = β A $^{\alpha}$) is shown for each subject as a function of amplitude as follows:

$$\begin{bmatrix} K_{sub1}(A) \\ K_{sub2}(A) \\ K_{sub3}(A) \\ K_{sub4}(A) \\ K_{sub5}(A) \\ K_{sub6}(A) \\ K_{sub7}(A) \\ K_{sub8}(A) \\ K_{sub9}(A) \\ K_{sub10}(A) \end{bmatrix} = \begin{bmatrix} 11.50 \\ 13.25 \\ 4.17 \\ 12.71 \\ 4.87 \\ 4.75 \\ 8.00 \\ 6.34 \\ 6.51 \\ 4.20 \end{bmatrix} \cdot A^{-0.11}$$

As illustrated in Figure 6, the regression lines from the above equation are parallel but have a random intercept for each subject. Note the high R^2 values for each regression model for the group of 10 subjects. The R^2 values refer to the fit of the model of the combined data for all subjects, with subject as a random factor and slope as a fixed factor, as illustrated by the above expanded version of the equation for stiffness. Setting subject as a random factor produced regression lines with subject specific intercepts (β) but with the same slope (α) for each mechanical parameter.

Insert Figure 6 here

4. Discussion

The joint mechanics changed markedly over the range of amplitudes studied. With an increase in displacement amplitude from 0.4° to 6° RMS (0.2% to 3% of FCR muscle length), the stiffness decreased by 31%, the viscosity decreased by 73%, the damping ratio decreased by 71% and the resonant frequency decreased from 10.5 Hz to 7.3 Hz. The changes were consistent with previous findings that both joint stiffness and viscosity decrease with increasing amplitude (Kearney and Hunter, 1982; Milner and Cloutier, 1998; Nichols, 1985). In this study, we have shown that the decreases in stiffness, viscosity, damping ratio and resonant frequency with increasing displacement amplitude can be described by power relationships. These relationships were consistent across all subjects and demonstrated excellent fit to the data through both the short range stiffness region and larger displacements. The models described here therefore provide normative data for the adult population and may be used in the modelling of human movement, in the study of neurological disorders of movement and in robotics where human movement is simulated.

The actual values of the mechanical parameters varied across subjects but are comparable with those reported previously. Milner and Cloutier (1993) determined wrist stiffness coefficients between 3.8 and 16 Nm.rad^{-1} and viscosity between 0 and 0.11 Nm.s.rad^{-1} at 15%MVC flexion for various oscillation amplitudes. In a later study, these workers reported damping coefficients at the wrist in the range of 0.06-0.075 Nm.s.rad^{-1} during voluntary movement (Milner and Cloutier, 1998). In the current study at 15%MVC, the wrist stiffness coefficients ranged between 2.63 and 16.44 Nm.rad^{-1} and damping coefficients ranged between 0.02 and 0.19 Nm.s.rad^{-1}. Other studies have reported stiffness coefficients at the wrist between 2-3 Nm.rad^{-1} for a contraction level of 5%MVC (De Serres and Milner, 1991; Gielen and Houk, 1984). Sinkjaer and Hayashi (1989) also reported values for wrist damping ratio and natural frequency comparable to values in the current study. The values of inertia were comparable with those derived from Winter's (1990) anthropometric tables. These tables can provide only a single estimate of inertia for each subject, whereas in the present study, values were computed for the six displacement amplitudes. These values were found to increase significantly between the short range region and larger amplitudes. This suggests that there was an increase in acceleration sensitivity at the larger displacements.

Previous studies have shown distinctive differences in stiffness for short range regions and larger displacements. Sinkjaer et al (1988) found that at a dorsiflexion contraction of 30%MVC, the stiffness of the ankle decreased between displacements of 1° to 2° and did not change from 2-7°, whereas Kearney and Hunter (1982) found a continuous but nonlinear decrease in stiffness and viscosity for displacements up to 14° at small ankle torques of 4-6 Nm. In the larger group of subjects studied here than in these previous studies, the consistent power relationships observed between displacement amplitude and mechanical parameters at the wrist more closely matched the findings of Kearney and Hunter.

The mechanical changes with displacement amplitude observed here cannot be attributed to the small changes that occurred in joint torque or muscle contraction levels. The reduction in net flexor torque was only 0.5 Nm, so the changes in muscle co-contraction would be more important in determining the mechanical properties of the joint. The largest contraction level was in FCR, which was maintained at the target level via feedback to the subjects, while the contraction levels in all other muscles increased with displacement amplitude. These small but uniform increases were probably caused by the increase in muscle afferent drive associated with greater displacement amplitude, since afferent input has a strong facilitatory influence on motorneurons (Macefield et al, 1993). The fact that the net flexor torque decreased indicates that the contraction level increases were relatively greater in the extensors than the flexors, perhaps because the feedback from FCR constrained the increase in the flexors (measured in μV, the increases were similar in extensors and flexors in the intramuscular recordings). Regardless of the underlying mechanisms, however, the result was an increase in muscle co-contraction which would be expected to produce an increase in joint stiffness (De Serres and Milner, 1991; Milner et al, 1995), rather than the decrease observed. Therefore, the decrease in joint stiffness with displacement amplitude is likely to have been underestimated by the small increase in co-contraction. A similar co-contraction effect would likely have been present in the earlier study by Kearney and Hunter (1982), where torque was controlled but no muscle activity was recorded.

The observed wrist joint mechanics hold particular functional implications for the stability and mobility of the neuromuscular system. For control of posture, a high resistance to small perturbations and damping of small oscillations are desirable. Voluntary movements, however, are typically of large amplitude and so a progressive decrease in both stiffness and damping with increasing amplitude facilitates a lively response of the neuromuscular system. Then, in maintaining limb position at the termination of voluntary movements, high resistance to small perturbations and damping of small oscillations are again required. Therefore, the observed mechanical properties of higher initial stiffness and viscosity which decrease progressively and nonlinearly as displacement amplitude increases may provide a good compromise between postural stability and liveliness of voluntary movements.

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References

Backdahl, M. and Carlsoo, S., 1961. Distribution of activity in muscles acting on the wrist. (An electromyographic study). Acta Morphol Neerl Scand, 4 136-144.

Basmajian, J. V. and Blumenstein, R., 1980. Electrode placement in emg biofeedback. Baltimore, Williams & Wilkins.

Bendat, J. S. and Piersol, A. G., 1971. Random data: Analysis and measurement procedures. New York, Wiley-Interscience.

Bennett, D. J., Hollerbach, J. M., Xu, Y. and Hunter, I. W., 1992. Time-varying stiffness of human elbow joint during cyclic voluntary movement. Experimental Brain Research, 88 (2), 433-42.

Campbell, K. S. and Lakie, M., 1998. A cross-bridge mechanism can explain the thixotropic short-range elastic component of relaxed frog skeletal muscle. Journal of Physiology, 510 (3), 941-962.

De Serres, S. J. and Milner, T. E., 1991. Wrist muscle activation patterns and stiffness associated with stable and unstable mechanical loads. Experimental Brain Research, 86 451-458.

de Vlugt, E., van der Helm, F. C., Schouten, A. C. and Brouwn, G. G., 2001. Analysis of the reflexive feedback control loop during posture maintenance. Biological Cybernetics, 84 (2), 133-41.

Gielen, C. C. and Houk, J. C., 1984. Nonlinear viscosity of human wrist. Journal of Neurophysiology, 52 (3), 553-569.

Hill, D. K., 1968. Tension due to interaction between the sliding filaments in resting striated muscle. The effect of stimulation. Journal of Physiology, 199 (3), 637-84.

Horii, E., An, K. N. and Linscheid, R. L., 1993. Excursion of prime wrist tendons. Journal of Hand Surgery - American Volume, 18 (1), 83-90.

Kearney, R. E. and Hunter, I. W., 1982. Dynamics of human ankle stiffness: Variation with displacement amplitude. Journal of Biomechanics, 15 753-756.

Kearney, R. E., Stein, R. B. and Parameswaran, L., 1997. Identification of intrinsic and reflex contributions to human ankle joint stiffness dynamics. IEEE Transactions on Biomedical Engineering, 44 (6), 493-504.

Kirsch, R. F., Boskov, D. and Rymer, W. Z., 1994. Muscle stiffness during transient and continuous movements of cat muscle: perturbation characteristics and physiological relevance. IEEE Transactions on Biomedical Engineering, 41 (8), 758-70.

Lambertz, D., Perot, C., Kaspranski, R. and Goubel, F., 2003. Influence of long-term spaceflight on neuromechanical properties of muscles in humans. Journal of Applied Physiology, 94 490-498.

Lieber, R. L., Fazeli, B. M. and Botte, M. J., 1990. Architecture of selected wrist flexor and extensor muscles. Journal of Hand Surgery - American Volume, 15 (2), 244-250.

Macefield, V. G., Gandevia, S. C., Bigland-Ritchie, B., Gorman, R. B. and Burke, D., 1993. The firing rates of human motoneurones voluntarily activated in the absence of muscle afferent feedback. Journal of Physiology, 471 429-443.

McFarland, G. B., Krusen, U. L. and Weathersby, H. T., 1962. Kinesiology of selected muscles acting on the wrist: electromyographic study. Archives of Physical Medicine and Rehabilitation, 43 165 - 171.

Milner, T. E. and Cloutier, C., 1993. Compensation for mechanically unstable loading in voluntary wrist movement. Experimental Brain Research, 94 522-532.

Milner, T. E. and Cloutier, C., 1998. Damping of the wrist joint during voluntary movement. Experimental Brain Research, 122 (3), 309-17.

Milner, T. E., Cloutier, C., Leger, A. B. and Franklin, D. W., 1995. Inability to activate muscles maximally during cocontraction and the effect on joint stiffness. Experimental Brain Research, 107 (2), 293-305.

Nichols, T. R., 1985. Autogenetic reflex action in tibialis anterior compared with that in soleus muscle in the decerebrate cat. Experimental Brain Research, 59 (2), 232-41.

Perreault, E., Crago, P. and Kirsch, R., 1998. Simultaneous estimation of the intrinsic and reflex contributions to muscle dynamics: a modeling study. Proceedings of the 20th Annual International Conference of the IEEE Engineering Medicine and Biology Society, 20 (5), 2346-9.

Rack, P. M. H. and Westbury, D. R., 1974. The short range stiffness of active mammalian muscle and its effect on mechanical properties. Journal of Physiology, 240 331-350.

Sinkjaer, T. and Hayashi, R., 1989. Regulation of wrist stiffness by the stretch reflex. Journal of Biomechanics, 22 1133-1140.

Sinkjaer, T., Toft, E., Andreassen, S. and Hornemann, B. C., 1988. Muscle stiffness in human ankle dorsiflexors: intrinsic and reflex components. Journal of Neurophysiology, 60 1110-1121.

Wiegner, A. W., 1987. Mechanism of thixotropic behavior at relaxed joints in the rat. Journal of Applied Physiology, 62 (4), 1615-1621.

Winter, D. A., 1990. Biomechanics and motor control of human movement. New York, Wiley-Interscience.

Zhang, L. Q. and Rymer, W. Z., 1997. Simultaneous and nonlinear identification of mechanical and reflex properties of human elbow joint muscles. IEEE Transactions on Biomedical Engineering, 44 (12), 1192-1209.

Table and Figure Captions

Table 1: VAF values representing the goodness of the fit of the models to the measured data for both gain and phase for all displacement amplitudes and all subjects.

VAF Gain	**0.4° RMS**	**0.5° RMS**	**0.6° RMS**	**2° RMS**	**4° RMS**	**6° RMS**	**Mean**
sub1	0.58	0.65	0.82	0.55	0.97	0.98	**0.76**
sub2	0.96	0.94	0.98	0.93	0.99	0.99	**0.97**
sub3	0.97	0.91	0.92	0.96	0.98	0.98	**0.95**
sub4	0.75	0.78	0.70	0.66	0.84	0.95	**0.78**
sub5	0.78	0.93	0.93	0.81	0.91	0.94	**0.88**
sub6	0.84	0.87	0.91	0.90	0.93	0.97	**0.90**
sub7	0.96	0.77	0.83	0.84	0.96	0.94	**0.88**
sub8	0.76	0.90	0.85	0.92	0.86	0.90	**0.87**
sub9	0.76	0.78	0.87	0.89	0.83	0.98	**0.85**
sub10	0.95	0.89	0.93	0.82	0.95	0.95	**0.92**
Mean	**0.83**	**0.84**	**0.87**	**0.83**	**0.92**	**0.96**	**0.88**

VAF Phase	**0.4° RMS**	**0.5° RMS**	**0.6° RMS**	**2° RMS**	**4° RMS**	**6° RMS**	**Mean**
sub1	0.99	0.98	1.00	0.97	0.98	1.00	**0.98**
sub2	0.99	0.99	0.99	0.97	0.98	0.97	**0.98**
sub3	1.00	0.97	0.98	0.98	0.97	0.99	**0.98**
sub4	0.98	0.99	0.99	0.93	0.95	0.98	**0.97**
sub5	0.98	0.98	0.98	0.98	0.98	0.94	**0.97**
sub6	0.98	0.98	0.98	0.97	0.99	0.99	**0.98**
sub7	0.99	0.99	0.98	0.93	0.94	0.97	**0.97**
sub8	0.98	0.95	0.98	0.95	0.91	0.97	**0.96**
sub9	0.96	0.99	0.99	0.97	0.98	0.99	**0.98**
sub10	0.97	0.99	0.97	0.98	0.99	0.96	**0.98**
Mean	**0.98**	**0.98**	**0.98**	**0.96**	**0.97**	**0.98**	**0.98**

Table 2: Individual subject values and group means and standard error of inertia, stiffness, viscosity, damping ratio and natural frequency. The inertia values estimated using Winter's tables (Winter, 1990) are also indicated for comparison with modelled values

		Displacement amplitude (RMS)						
		0.4°	**0.5°**	**0.6°**	**2°**	**4°**	**6°**	**Winter**
Inertia I (x 10^{-2} kg.m^{-2})	sub1	0.22	0.19	0.17	0.28	0.39	0.38	0.39
	sub2	0.56	0.47	0.54	0.49	0.52	0.52	0.45
	sub3	0.20	0.23	0.21	0.20	0.20	0.21	0.20
	sub4	0.37	0.39	0.39	0.33	0.49	0.54	0.39
	sub5	0.15	0.16	0.19	0.21	0.19	0.17	0.17
	sub6	0.12	0.10	0.13	0.14	0.17	0.17	0.16
	sub7	0.15	0.16	0.19	0.28	0.34	0.30	0.28
	sub8	0.15	0.15	0.13	0.23	0.21	0.20	0.19
	sub9	0.11	0.16	0.16	0.20	0.21	0.21	0.16
	sub10	0.09	0.09	0.10	0.13	0.14	0.11	0.11
	Mean	**0.21**	**0.21**	**0.22**	**0.25**	**0.28**	**0.28**	**0.24**
	SE	**0.05**	**0.04**	**0.04**	**0.03**	**0.04**	**0.05**	**0.04**
Stiffness K (Nm.rad^{-1})	sub1	13.01	11.62	10.59	10.19	11.42	10.20	
	sub2	16.44	13.74	15.99	11.89	11.22	9.19	
	sub3	5.00	5.38	4.64	4.10	3.22	2.63	
	sub4	14.49	15.10	14.35	9.63	11.01	10.40	
	sub5	5.83	5.18	5.56	5.66	3.93	2.92	
	sub6	5.43	4.49	4.91	4.26	4.45	4.16	
	sub7	8.16	8.21	7.70	7.67	8.08	6.71	
	sub8	7.50	6.96	6.24	7.60	5.29	4.07	
	sub9	5.52	6.87	6.51	6.50	6.69	5.80	
	sub10	4.45	4.19	3.91	4.57	4.42	3.06	
	Mean	**8.58**	**8.17**	**8.04**	**7.21**	**6.97**	**5.91**	
	SE	**1.39**	**1.25**	**1.33**	**0.85**	**1.02**	**0.97**	
Viscosity B (Nm.s.rad^{-1})	sub1	0.19	0.17	0.17	0.11	0.06	0.04	
	sub2	0.12	0.11	0.12	0.09	0.06	0.06	
	sub3	0.07	0.06	0.06	0.03	0.03	0.02	
	sub4	0.18	0.18	0.19	0.14	0.08	0.06	
	sub5	0.08	0.09	0.09	0.04	0.02	0.03	
	sub6	0.08	0.08	0.07	0.04	0.02	0.02	
	sub7	0.15	0.14	0.12	0.08	0.06	0.05	
	sub8	0.11	0.12	0.10	0.06	0.05	0.03	
	sub9	0.09	0.09	0.08	0.05	0.03	0.03	
	sub10	0.08	0.07	0.07	0.03	0.02	0.02	
	Mean	**0.11**	**0.11**	**0.11**	**0.07**	**0.04**	**0.03**	
	SE	**0.01**	**0.01**	**0.01**	**0.01**	**0.01**	**0.01**	
Damping Ratio DR	sub1	0.56	0.56	0.64	0.34	0.14	0.10	
	sub2	0.20	0.22	0.20	0.18	0.13	0.14	
	sub3	0.35	0.27	0.31	0.18	0.17	0.15	
	sub4	0.39	0.37	0.40	0.39	0.17	0.12	
	sub5	0.45	0.50	0.43	0.19	0.14	0.21	
	sub6	0.46	0.58	0.44	0.26	0.13	0.11	
	sub7	0.68	0.60	0.49	0.27	0.17	0.16	
	sub8	0.50	0.58	0.57	0.23	0.22	0.14	
	sub9	0.55	0.42	0.41	0.24	0.15	0.12	
	sub10	0.61	0.59	0.57	0.23	0.11	0.14	
	Mean	**0.48**	**0.47**	**0.45**	**0.25**	**0.15**	**0.14**	
	SE	**0.04**	**0.04**	**0.04**	**0.02**	**0.01**	**0.01**	
Natural Frequency W_n (Hz)	sub1	12.2	12.3	12.4	9.7	8.7	8.3	
	sub2	8.6	8.6	8.6	7.8	7.4	6.7	
	sub3	8.0	7.7	7.5	7.2	6.4	5.6	
	sub4	10.0	9.9	9.7	8.6	7.6	7.0	
	sub5	9.8	9.1	8.7	8.4	7.3	6.6	
	sub6	10.5	10.9	9.8	8.9	8.2	7.9	
	sub7	11.7	11.5	10.0	8.3	7.7	7.5	
	sub8	11.4	10.9	11.0	9.1	8.0	7.1	
	sub9	11.2	10.3	10.0	9.2	9.0	8.3	
	sub10	11.2	10.9	10.2	9.5	9.0	8.3	
	Mean	**10.5**	**10.2**	**9.8**	**8.7**	**7.9**	**7.3**	
	SE	**0.4**	**0.4**	**0.4**	**0.2**	**0.3**	**0.3**	

Table 3: The values for α and the mean and range of values for β for each mechanical parameter in the mathematical relationships between joint mechanics and displacement amplitude.

MP	**β mean (range)**	**α**
K ($Nm.rad^{-1}$)	6.94 (4.17 – 13.25)	-0.11
B ($Nm.s.rad^{-1}$)	0.08 (0.05 – 0.14)	-0.47
Damping ratio	0.32 (0.20 – 0.39)	-0.48
W_n (Hz)	9.26 (7.27 – 10.83)	-0.12

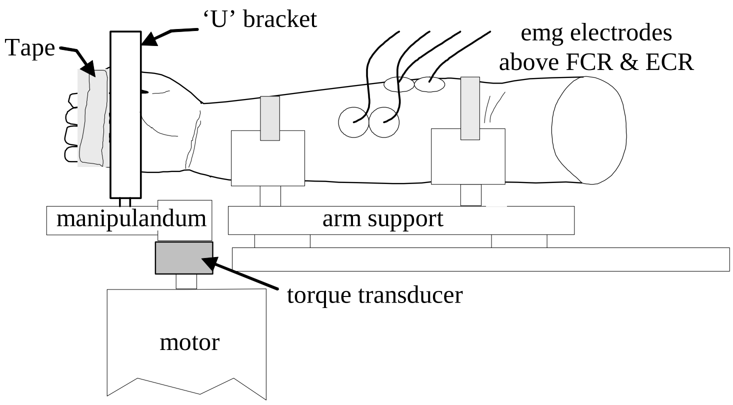

Figure 1: Experimental set-up.

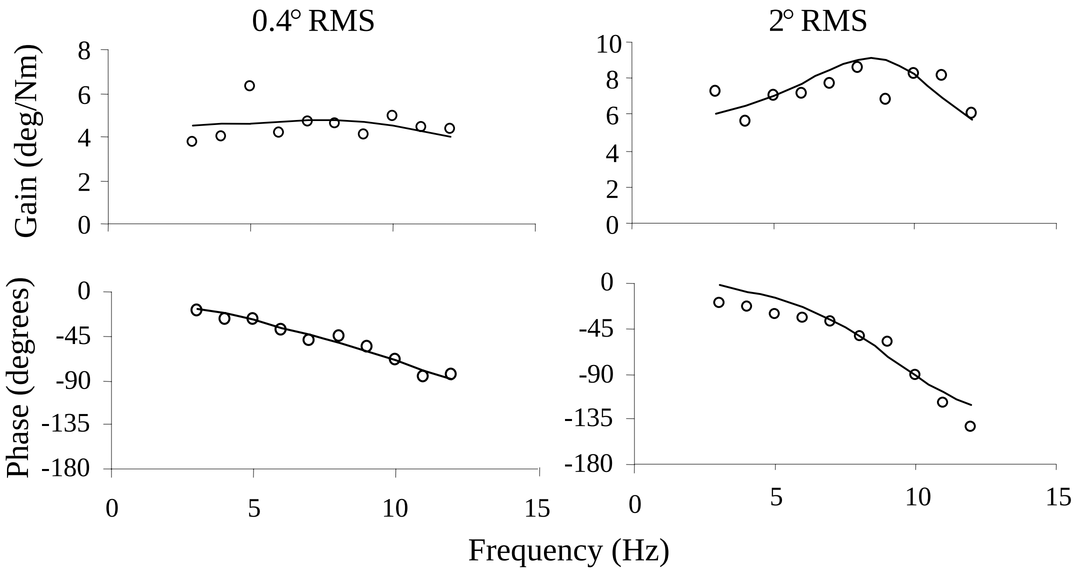

Figure 2: Measured (o) and modelled (solid line) gain and phase for 0.4° and 2° RMS displacement amplitudes for Subject 1, who had the lowest VAFs observed in the study (cf, Table 1).

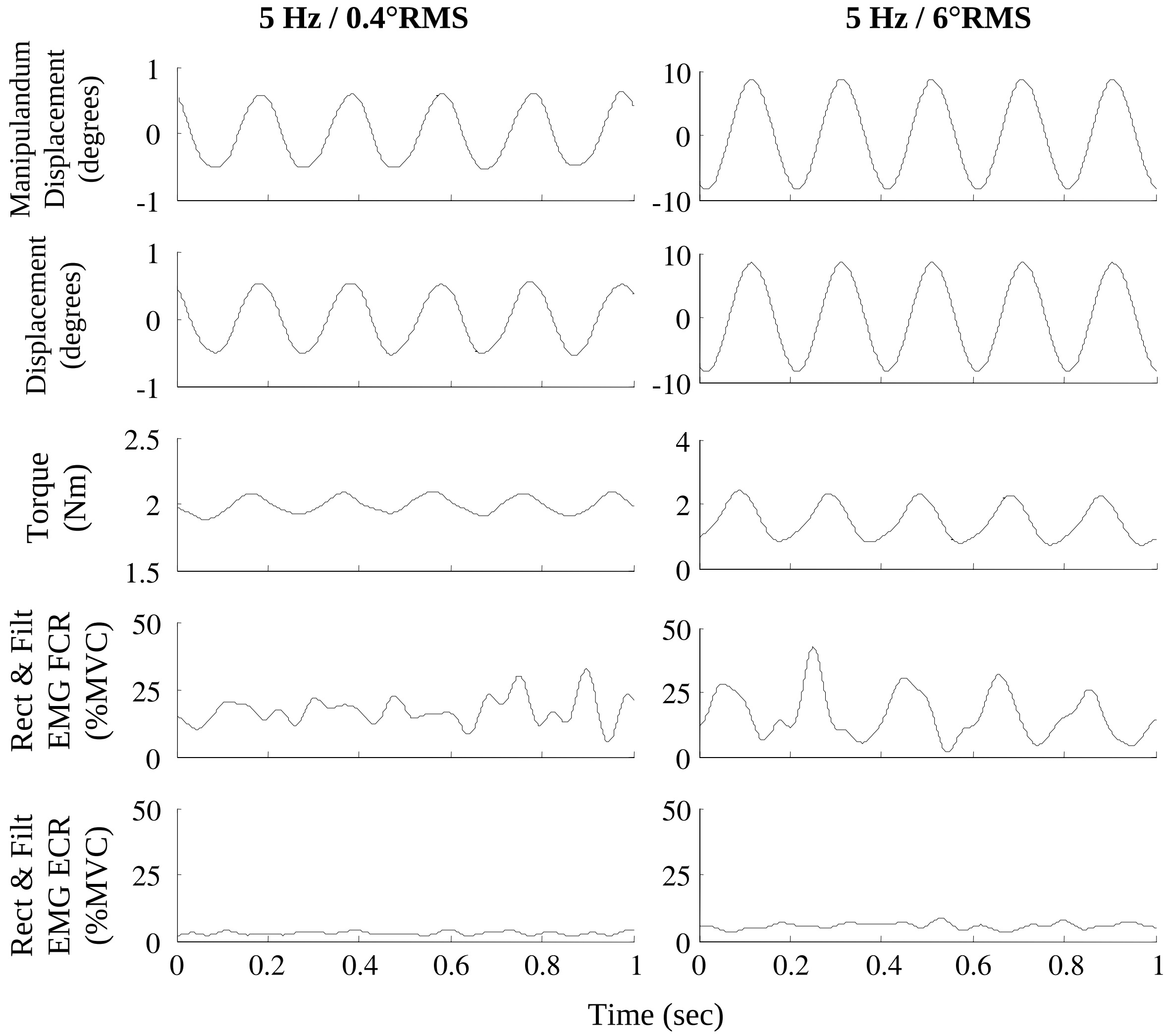

Figure 3: Raw data from Subject 1 indicating, from top down, displacement of the manipulandum alone, displacement of manipulandum + wrist, torque of manipulandum + wrist, rectified and filtered EMG (20 Hz cut-off, 8th-order Butterworth) from FCR and ECR for the 0.4°RMS and 6°RMS displacements at 5 Hz. Note the different scaling for the displacement and torque signals for the 0.4°RMS and 6°RMS displacements.

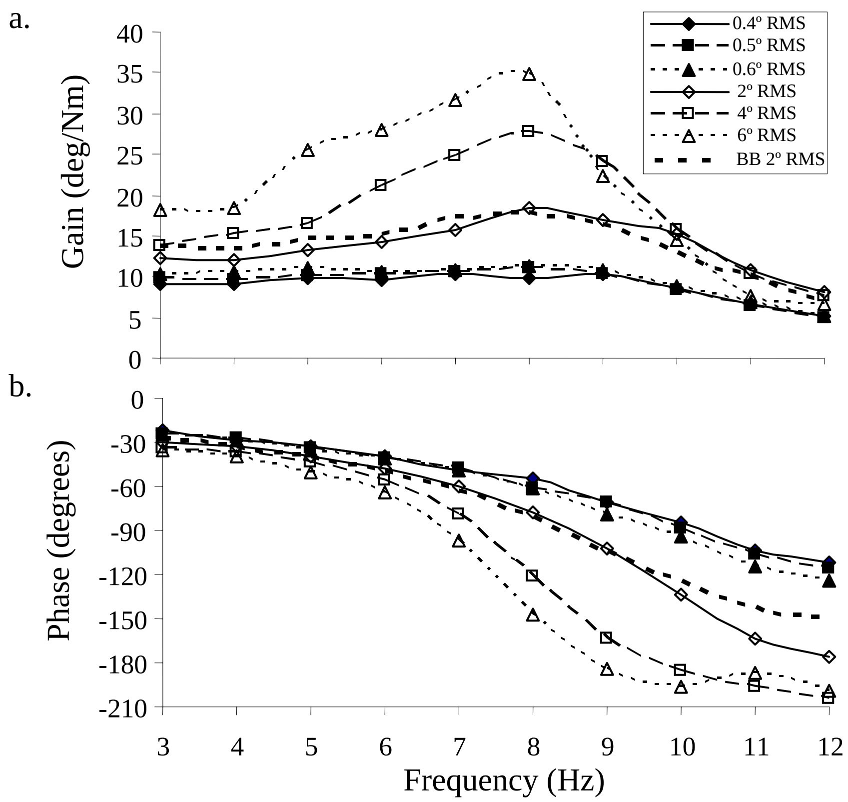

Figure 4: Group average (a) gain and (b) phase vs frequency for the six displacement amplitudes with the sinusoidal signals and a single broad bandwidth signal at 2° RMS amplitude.

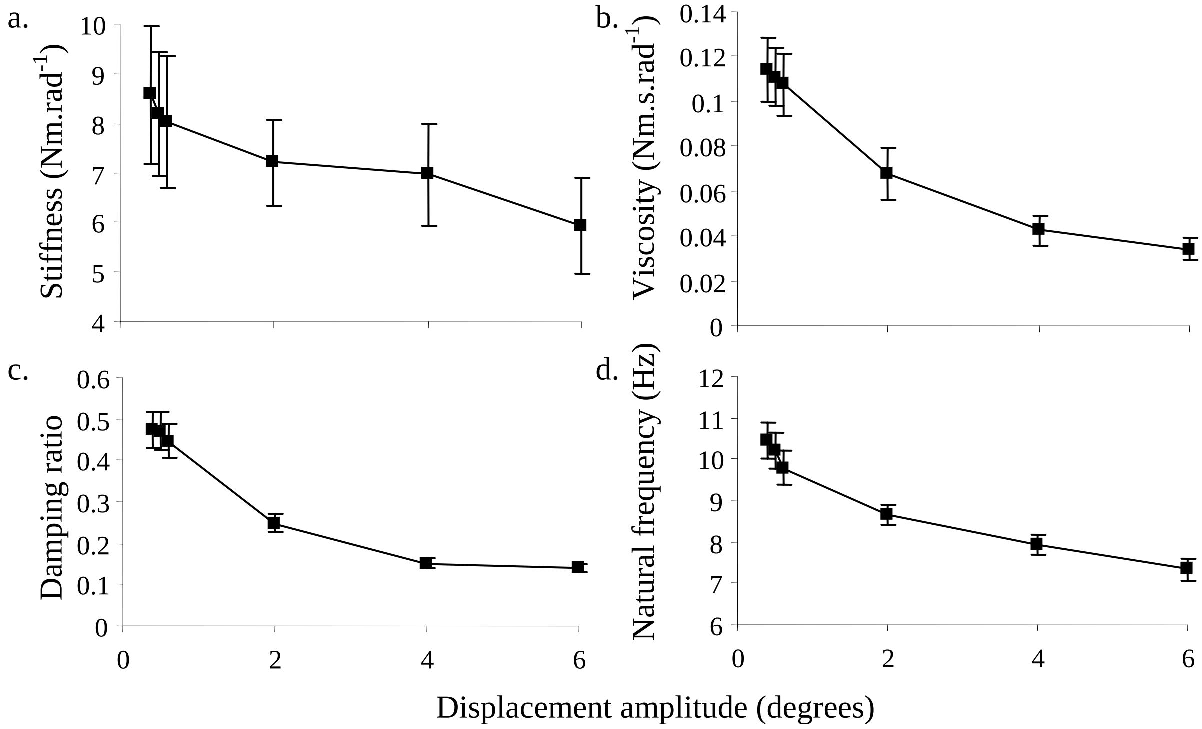

Figure 5: Average (± standard error) across all subjects for (a) stiffness, (b) viscosity, (c) damping ratio and (d) natural frequency versus displacement amplitude.

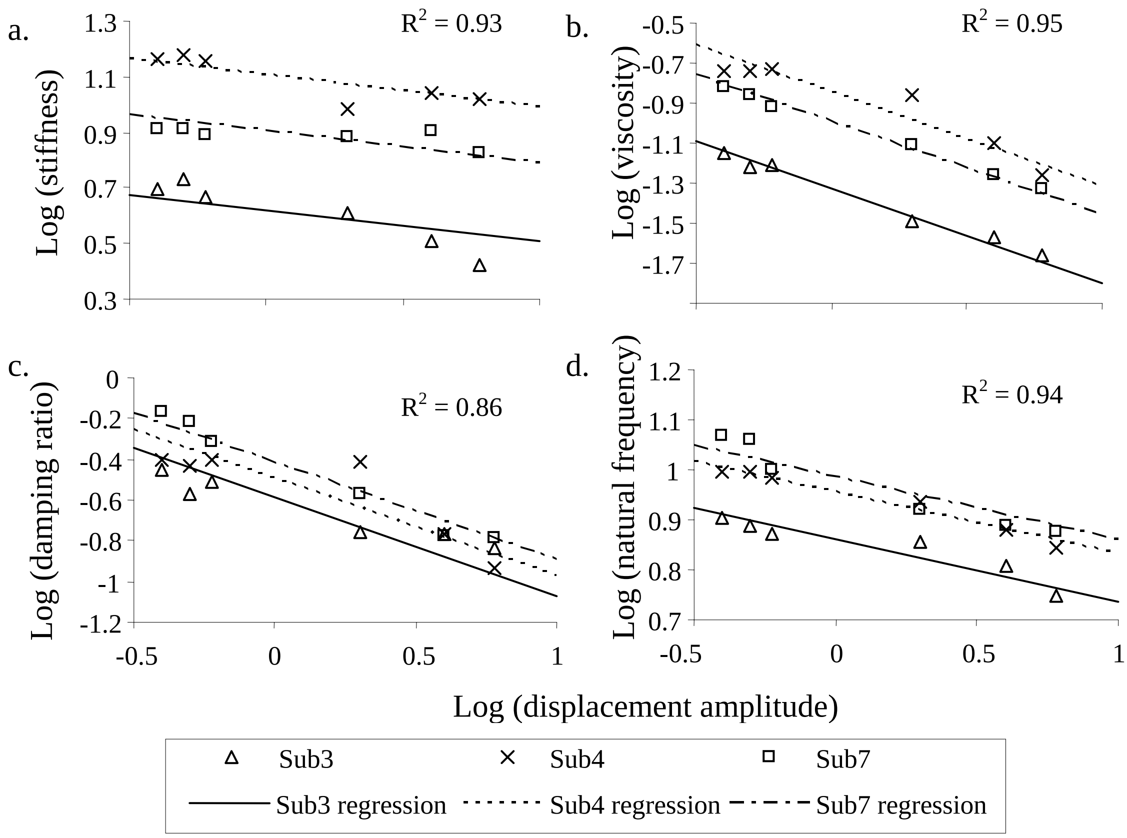

Figure 6: (a) Log(stiffness), (b) log(viscosity), (c) log(damping ratio) and (d) log(natural frequency) versus log(displacement amplitude) and linear regression lines for 3 subjects. The R^2 values show the variance across all subjects accounted for by the random subject factor model. For each mechanical parameter, the intercept is different for each subject but the slope of the regression line is the same for every subject. Note: Subject 4 had one of the lowest average VAFs (cf, Table 1).