RESEARCH ARTICLES

Antonia F. de C. Hamilton · Kelvin E. Jones ·
Daniel M. Wolpert

The scaling of motor noise with muscle strength and motor unit number in humans

Abstract Understanding the origin of noise, or variability, in the motor system is an important step towards understanding how accurate movements are performed. Variability of joint torque during voluntary activation is affected by many factors such as the precision of the descending motor commands, the number of muscles that cross the joint, their size and the number of motor units in each. To investigate the relationship between the peripheral factors and motor noise, the maximum voluntary torque produced at a joint and the coefficient of variation of joint torque were recorded from six adult human subjects for four muscle/joint groups in the arm. It was found that the coefficient of variation of torque decreases systematically as the maximum voluntary torque increases. This decreasing coefficient of variation means that a given torque or force can be more accurately generated by a stronger muscle than a weaker muscle. Simulations demonstrated that muscles with different strengths and different numbers of motor units could account for the experimental data. In the simulations, the magnitude of the coefficient of variation of muscle force depended primarily on the number of motor units innervating the muscle, which relates positively to muscle strength. This result can be generalised to the situation where more than one muscle is available to perform a task, and a muscle activation pattern must be selected. The optimal muscle activation pattern required to generate a target torque using a group of muscles, while minimizing the consequences of signal dependent noise, is derived.

A. F. de C. Hamilton (✉)
Institute of Cognitive Neuroscience,
Alexandra House, 17 Queen Square,
London, WC1N 3AR, UK
e-mail: a.hamilton@ion.ucl.ac.uk
Tel.: +44-20-76791138
Fax: +44-20-78132835

K. E. Jones
Department of Biomedical Engineering, Research Transition
Facility, University of Alberta,
Edmonton, Alberta, T6G 2V2, Canada

D. M. Wolpert
Sobell Department of Motor Neuroscience and Movement
Disorders, Institute of Neurology, University College London,
Queen Square,
London, WC1N 3BG, UK

Introduction

Noise or variability is an unavoidable feature of voluntary muscle contraction and influences the accuracy of every movement a person makes. The importance of motor noise was demonstrated by Fitts (1954), who showed that movements cannot be both fast and precise: there is a speed-accuracy trade-off. Schmidt et al. (1979) demonstrated that as the force produced by a subject increases, the standard deviation of the force increases in a linear fashion. Both of these results can be explained by the presence of signal-dependent noise in muscle force generation, that is noise whose standard deviation increases linearly with the mean (constant coefficient of variation). This noise has been shown to arise from the orderly recruitment and firing rate variability found in the motor neuron pool innervating muscles (Jones et al. 2002). At the motor unit level there are two sources of noise: (1) ripple, associated with an unfused contraction and time-locked to each motor neuron spike; and (2) slow frequency, associated with the stochastic discharge of the motor neurons.

It has recently been proposed that reducing the consequences of signal-dependent noise is a fundamental strategy in human motor control (Task Optimisation in the Presence of Signal Dependent noise, TOPS; Harris and Wolpert 1998). The presence of noise in the motor system means that every movement we make will have some inaccuracy. However, different trajectories from the set of all possible trajectories that can achieve a task may have different error distributions. Under the TOPS strategy, the motor system picks the trajectory that minimises the

consequences of signal dependent noise in the relevant task dimension. For example, to reach to a target, the optimal trajectory under TOPS is the trajectory with the least end point variance. Harris and Wolpert (1998) demonstrated that this optimal hand trajectory is nearly straight with a bell-shaped velocity profile, matching the hand paths shown by people performing the same task (Morasso 1981; Abend et al. 1982). Use of the TOPS strategy is also able to account for the stereotyped trajectories observed in ellipse drawing and eye movements (Harris and Wolpert 1998) and in obstacle avoidance movements (Hamilton and Wolpert 2002).

At the force level, muscle activation patterns are redundant, that is more than one muscle activation pattern can be used to achieve the same joint torque. For example, extensor carpi radialis and extensor carpi brevis are muscles acting to extend the wrist, so a desired level of net extension torque could be achieved by activating either one of these muscles or any combination. Despite this redundancy, the muscle activation patterns used in a movement show stereotypy across subjects and across repeated trials. Descriptions of the function of different muscles (for example, Basmajian 1978) implicitly rely on the similarity of muscle activation patterns between subjects. Muscle activity in specific tasks shows stereotypy whether subjects generate force with the fingertips (Valero-Cuevas et al. 1998), the wrist (Hoffman and Strick 1999), the neck (Vasavada et al. 2002) or the arm (van Zuylen et al. 1988; Flanders and Soechting 1990; Buchanan et al. 1993; van Bolhuis and Gielen 1997). This is despite the large number of degrees of freedom available in these systems, for example, 23 neck muscles to control three directions of force generation. Primates also show repeatable patterns of muscle activation when grasping the same object repeatedly, and different activation patterns for different objects (Brochier et al. 2001). This suggests that stereotypy is a general characteristic of movement and is not unique to humans.

Various cost functions have been proposed to explain why particular patterns of muscle activation are found in particular tasks. MacConaill (1967) suggested that the motor system might activate muscles in order to minimise the total muscle force required to produce a desired torque (force multiplied by moment arm), meaning that the muscles with the largest moment arm should be fully activated before muscles with a smaller moment arm are used. However, both empirical data (Basmajian and Latif 1957) and simulations (Yeo 1976) suggest this cost function is not used in the motor system. Some investigators have proposed cost functions based on fatigue or endurance (Pedotti et al. 1978; Crowninshield and Brand 1981; Dul et al. 1984a, 1984b). In contrast, several studies suggest that either total muscle force squared or muscle stress (force divided by physiological cross sectional area) squared should be minimised, for both upper limb (van Bolhuis and Gielen 1999; Gomi 2000) and lower limb muscles (Pedotti et al. 1978). Similarly, a cost function based on a combination of muscle effort (activation squared) and accuracy has been

suggested to account for wrist muscle recruitment (Fagg et al. 2002).

All these cost functions are mathematically similar, and none has been shown to be clearly superior to any of the others (Collins 1995; van Bolhuis and Gielen 1999). The TOPS strategy proposes that goal-directed movements should be optimised to reduce the consequences of signal-dependent noise, and we suggest that the same principle should apply to the selection of muscle activation patterns for accurate movement. For example, if the two muscles mentioned above acting to extend the wrist contribute different amounts of noise, the motor system should choose to activate less noisy muscles before it activates noisier muscles in order to make accurate movements. However, it is not known how the level of noise varies across different muscles—do stronger muscles generate more or less noise than weaker muscles for the same output force?

The purpose of this study is to investigate the relationship between the strength of a muscle, the number of motor units in a muscle and the level of noise produced by the muscle, and thus to define a cost function specifying which muscles should be used to generate a joint torque with the least noise. First, we experimentally determine how torque variability changes in relation to the maximum voluntary torque (MVT) produced at four joints in the human hand and arm. We cannot experimentally relate the variability of force produced by a single muscle to its size or strength because we cannot separate the action of a single muscle at each joint from its agonists. However, because the torques produced at a joint by a set of agonist muscles will sum linearly, we consider the measured MVT and torque variability as representative of the strength and noise of a 'virtual' muscle incorporating all the agonists acting at the joint studied. Thus we refer to muscle noise or joint noise, and muscle strength or joint strength interchangeably throughout, and the validity of this assumption is considered in the "Discussion". We also use simulations to investigate how the noise in muscle force or joint torque changes with the number of motor units innervating a muscle. Thus we are able to relate the coefficient of variation of joint torque to that joint's maximum torque and to the number of motor units involved in generating the torque.

Using this data, we will be able to distinguish between two competing hypotheses. It is possible that weaker muscles are less noisy, if for a given level of torque output, they activate more (weaker) motor units and thus generate less variability. Alternatively, motor noise might follow the same distribution as proprioceptive noise, which is smallest (in angular terms) in the most proximal joints (Hall and McCloskey 1983; Refshauge et al. 1995). As proximal muscles tend to be stronger, this would imply that strong muscles are less noisy than more distal, weaker muscles. These two hypotheses will be tested experimentally, and the causes of differences in variability between muscles investigated by simulations.

Methods

Torque generation experiment

Six right-handed healthy adult subjects aged between 22 and 35 years gave their informed consent to take part in this experiment, which was approved by the local ethics committee in accordance with the 1964 Declaration of Helsinki. For each subject, isometric torque and torque variability were recorded at four joints in the right upper limb. The joints were chosen to reflect a variety of muscle sizes, with as few muscles as possible acting about each joint. The four joint actions and muscles studied were: extension of the distal joint of the thumb (extensor pollicus longus), abduction of the first finger (first dorsal interosseous), flexion of the wrist (flexor carpi radialis, flexor carpi ulnaris, palmaris longus, flexor digitorum superficialis, flexor digitorum profundus) and extension of the elbow (triceps and anconeus). The estimated physiological cross sectional areas (PCSA) of the muscles acting at these joints are: thumb: 1.9 cm^2, finger: 4.1 cm^2, wrist: 12.2 cm^2, elbow: 21.5 cm^2 (data summed from An et al. 1981; Chao et al. 1989). In each case, the arm was secured so that only the joint of interest was free to generate torque, and a force transducer (FT) was use to record isometric force production in the direction of interest. The force output was converted to joint torque by multiplying by the distance from the centre of rotation of the joint to the FT. Locations of the FT and restraining straps to prevent movement of other joints are illustrated in Fig. 1.

For each muscle tested, the procedure was the same. Once the subject was seated comfortably and the FT positioned appropriately, three trials were performed to measure the MVT of the tested joint. During each trial, force data was recorded at 250 Hz and converted to a joint torque. The current torque level was displayed on a computer monitor in front of the subjects as a narrow vertical line which moved rightwards with increasing torque. Each subject was asked to generate the maximum torque he or she could for 10 s, while receiving visual feedback and verbal encouragement. Subjects rested for at least 1 min and often longer between each MVT trial to prevent fatigue. On MVT trials, it was found that subjects sometimes produced a large torque at first which gradually declined, but on other trials the torque developed slowly to the maximum level. To take account of this, MVT was calculated as the mean of the 1,000 highest points on each trace (not necessarily consecutive points), equivalent to 4 s of data.

Subjects then performed 36 torque matching trials. On each trial, the target torque was displayed as a fixed vertical line and feedback of the actual torque produced was displayed as a vertical line of a different colour which moved rightwards with increasing torque. The display was scaled so that −10% MVT was at the left edge of the screen, 0% MVT was marked with a fixed vertical line in a third colour, and 70% MVT was on the right of the screen. Thus the scaling on the screen remained constant for each muscle, but varied between muscles according to the MVT of that muscle. Different scaling was necessary for each muscle to ensure that different levels of noise were not due to differences in the resolution of the visual display between different muscles. Subjects were asked to match the target as accurately as possible, so that the target line and the feedback line (each 1 pixel wide) were superimposed. Visual feedback was provided for 7 s, then the feedback line vanished (target and zero lines remained visible) and subjects were instructed to maintain the target torque level as accurately as possible for a further 8 s. The final 10 s of torque data from each trial were saved to disk at 250 Hz. After each trial subjects were informed of their root mean squared error over the 8 s without feedback and asked to keep this value as low as possible. Subjects rested for at least 2 s between every trial, and could rest for longer if they chose. Six trials were performed at each of six torque levels from 5% MVT to 55% MVT in increments of 10% MVT, tested in a random order.

For data analysis, the final 8 s of each trial, i.e. the torque generated without visual feedback, was high pass filtered to remove the slow drift due to the absence of vision (3rd order Butterworth filter at 0.5 Hz). The mean of the unfiltered trace and the standard
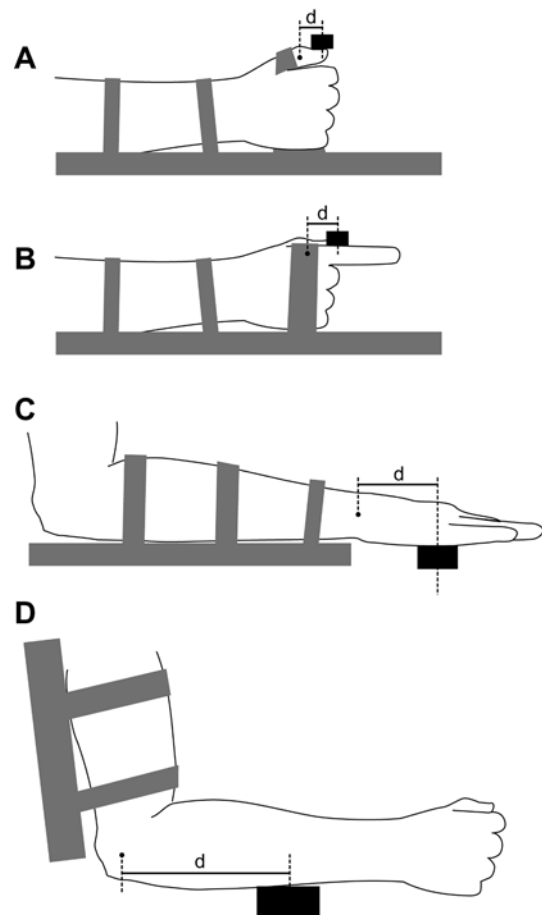

Fig. 1A–D Arm postures studied. In each plot, the *black rectangle* indicates the force transducer (*FT*) which was clamped in place (clamp not shown). The table top and restraining straps are shown in *grey*. *d* indicates the distance from the centre of rotation of the joint to the FT. **A** Configuration for measuring extension of the distal joint of the thumb. The lower arm was strapped to the table, the fingers clasped a specially shaped post and the proximal joint of the thumb was strapped to the top of the post. Subjects pressed up on the FT using only the distal joint of the thumb. **B** Configuration for measuring abduction of the first finger. The index finger pointed forward while the remaining fingers grasped a post and the hand was strapped to the post. The lower arm was also secured to the table. Subjects pressed up on the FT with the proximal interphalangeal joint of the index finger. **C** Configuration for measuring flexion of the wrist. The lower arm was secured to the table in a pronated posture and the subject pressed down on the FT with the palm of the hand. **D** Configuration for measuring extension of the elbow. The upper arm was tightly strapped to the back of the chair, and the shoulder and body held in place with seatbelts. Subjects pressed down on the FT with the lower arm

deviation (SD) of the filtered trace were calculated for each trial. Linear regression was performed on the data from all target matching trials to obtain the coefficient of variation (CV=SD/mean) for that muscle. Note that CV is a dimensionless variable and is the same whether it is calculated based on %MVT or absolute torque or the raw force output of the FT, because both SD and mean are measured in the same units. For the same reason, the CV of joint torque will be the same as the CV of muscle force for the muscle(s) which generated the torque. Thus possible inaccuracy in the measurement of MVT, for example, due to imprecision in measuring the distance from the centre of rotation of the joint to the force transducer, cannot influence the accuracy of the measured CV. As the task was isometric, differences in damping due to inertia at the

different joints also cannot influence the CV. To examine the relationship between muscle strength or MVT, and muscle noise or CV, these data were plotted on log-log axes. A linear regression to the natural log (ln) data for each subject was used to obtain the parameters c and k in:

$$ln(CV) = k\,ln(MVT) + c \qquad (1)$$

which is equivalent to the power law:

$$CV = \exp(c)MVT^{k} \qquad (2)$$

The parameters c and k define the relationship between muscle strength and muscle noise for each subject studied.

The muscle model

The relationship between the number of motor units in a muscle and muscle noise was examined using a previously tested model of force generation by a single muscle under isometric conditions (Fuglevand et al. 1993; Jones et al. 2002). This model has been described in detail in other papers (Fuglevand et al. 1993; Jones et al. 2002), so only a brief description will be given here. The muscle is modelled as a set of motor units, where recruitment threshold, firing rate and twitch force of each unit are related in an orderly fashion (Hennemann 1957; Henneman et al. 1965; Somjen et al. 1965). An activation function determines how many units are recruited and their mean firing rate for a particular input activation. Specifically, the recruitment threshold (RTE) of each neuron was defined by an exponential:

$$RTE_i = \exp(lnRR * i/n) \qquad (3)$$

(from Eq. 1 of Fuglevand et al. 1993), where RR is the range of recruitment thresholds, i is the index of the neuron, and n is the total number of motor neurons in the pool. This has the effect that a large number of units have a low threshold, with fewer high threshold units, and that recruitment is complete at the same point (in terms of % maximum force) for pools of different sizes. Similarly, the twitch force and contraction time of each unit were assigned according to exponential relationships (Eqs. 13 and 15 of Fuglevand et al. 1993),

such that the first unit to be recruited had the weakest and slowest twitch, and the last had the largest and fastest twitch. We chose to maintain a constant range of twitch forces regardless of the number of motor units in the pool, such that the last unit recruited always had a twitch force 100 times greater than that of the first unit recruited. Thus adding motor units to the pool is equivalent to interpolating extra points into the existing distribution of recruitment thresholds and twitch forces found in the motor unit pool. In this way, it is possible to simulate motor neuron pools of different sizes without altering the fundamental distribution of recruitment and force generating properties of motor units between each pool. Note that the actual twitch force values were scaled between simulations of muscles of different sizes to achieve a realistic maximum voluntary torque for each simulated muscle (as described below), but the distribution of twitch force values was held constant. The distribution of recruitment thresholds and contraction times across the pool were held constant in the same manner. Additional simulations were performed to check the sensitivity of the model to changes in the range of recruitment thresholds in different muscles and the effect of recruitment strategy on muscle noise.

For each motor unit that is recruited, a spike train with a Gaussian interspike interval distribution was generated and each spike caused a muscle twitch. The total muscle force was calculated as the sum of all the twitches in all the motor units, giving a force trace. It has been shown that the simulated force traces have the same variability characteristics as human isometric force generation (Jones et al. 2002), that is, the model shows a constant coefficient of variation during normal voluntary contraction over most of the force range. The increase in CV at very low forces observed by Galganski et al. (1993), Enoka et al. (1999) and others was also simulated by Jones et al. (2002) and reasons for this result will be considered in the "Discussion".

The influences of two free parameters of the muscle model were examined. First, the number of motor units (MUN) was varied to span the range found in human muscles: settings were 80, 160, 320, 640 and 1,280 motor units (Feinstein et al. 1955; McComas 1998). As described above, recruitment and twitch properties of the motor neuron pool were held constant across the different numbers of motor units. Second, we varied the spike train noise, that is, the coefficient of variation of the interspike interval distribution of each spike train: settings were 0.2, 0.4 and 0.6 to reflect the individual differences in spike train variability reported by Nordstrom and Miles (1991). Changes in these two parameters do not have an effect on the linear relationship between mean force and standard deviation of force characteristic of human isometric force production (Jones et

Table 1 Mean number of motor units and maximum torque for different muscles. Sources for motor unit numbers are: *Bu* Buchanan et al. (1993), *Ch* Christensen (1959), *Dc* de Carvalho (1976), *Fn* Feinstein et al. (1955), *Ku* Kuwabara et al. (1999), *Mc* McComas (1998). Where two sources are given, a simple mean MUN was calculated (without regard to the number of subjects in each source).

Maximum voluntary torque for most muscles was taken from the tabulated data in Winters and Stark (1988), but for the three hand muscles listed (first three entries) it was calculated from the physiological cross sectional area (Chao et al. 1989) and the neutral moment arm (Brand 1985) as described in the "Methods"

Muscle	Mean number of motor units		Maximum torque (Ncm)
First lumbrical	95.5	Fn	0.171
First dorsal interosseous	119.0	Fn	0.922
Abductus pollicus brevis	178.0	Ku	0.990
Vastus medialis	224.0	Mc	60.0
Gracialis	275.0	Ch	3.2
Plantaris	290.1	Mc Dc	4.5
Brachioradialis	332.5	Fn	10.0
Tibialis anterior	350.5	Mc Fn	37.0
Biceps	441.5	Mc Bu	9.0
Rectus femoris	609.0	Ch	45.0
Gastrocnemius medialis	678.5	Fn Ch	32.0
Semitendinosus	712.0	Ch	20.0
Sartorius	740.0	Ch	6.0

al. 2002), that is, the model continues to show a constant coefficient of variation. Fifteen simulations were performed to test all combinations of these parameters, and each was replicated three times. For each simulation, 30 force traces were generated covering the range of input activations, and the mean and standard deviation of these traces were used to calculate the coefficient of variation of force produced by that model. For each set of simulations with the same level of spike train noise, the relationship between the number of motor units and the coefficient of variation was determined by linear regression.

The force output of the muscle model is in arbitrary units, so in order to compare the model performance to the measured joint torques, we estimated the relationship between the number of motor units in a muscle (MUN) and the maximum voluntary torque (MVT) produced by that muscle at a joint. The number of motor units in human muscles can be estimated from postmortem counts of muscle fibres (Feinstein et al. 1955; Christensen 1959) combined with estimates of innervation number distributions, or in the case of a few groups of muscles from motor unit number estimation, MUNE (McComas 1998; Kuwabara et al. 1999). MUNE is an electrophysiological test mainly used in the study of amylotropic lateral sclerosis/motor neuron disease and has most often been used with the thenar muscle group and first dorsal interosseous (Stein and Yang 1990; Chan et al. 2001). Definitive values of the number of motor units in all normal human muscles do not exist, but counts for 13 muscles from a variety of sources are summarised in Table 1.

For ten of these muscles, the maximum torque produced by each muscle was taken from Winters and Stark (1988). The other three muscles were in the hand, and MVT for these was calculated from PCSA and neutral moment arm (nma) data (Brand 1985; Chao et al. 1989) according to: MVT (Ncm)=50 (Ncm^{-2}) PCSA (cm^2) nma (cm) (adapted from Winters and Stark 1988) and converted to Nm. It is important to take a neutral moment arm midway through the range of motion, and make the simplifying assumption that this is constant for all joint angles, because this parameter will be used in a regression with MUN which does not change with joint angle. All the values of MVT are also given in Table 1. Using the MUN and MVT values listed in Table 1, linear regression on the natural log of MUN and of MVT was used to obtain the power law:

$$MVT = \exp(-9.17)MUN^{1.92} \qquad (4)$$

which had an r^2 of 0.53 (p=0.0044). This relationship is plotted in Fig. 4A, and the power law was used to estimate the MVT which would be expected if each of the simulated muscles were a muscle in the human body. The relationship between MVT and CV could then be obtained for the simulation results in the same way as the experimental results.

Strong and weak muscle simulations

Simulations were also used to investigate the relative importance of three factors influencing output variability: the firing rate of the motor units, the number of motor units active and the recruitment range of the muscle. Two sets of detailed simulations were carried out comparing the performance of a strong muscle (320 motor units, MVT=6.79 Nm) and a weak muscle (160 motor units, MVT=1.79 Nm). The torque output of each model, in arbitrary units, was scaled so that the maximum was equal to the MVT of that muscle, as predicted by the power law relating MUN to MVT described above. A constant spike train noise of 0.2 was used for both muscles, and all other parameters, including the range of twitch forces and recruitment thresholds, were identical. Each muscle was activated at a range of excitations, and the torque output of the whole muscle and firing rate of each unit was saved. Finally, the impact of different recruitment strategies on motor noise was examined by varying recruitment from all units at once to a 100-fold range of thresholds, in both the strong and weak muscles.

Results

Experimental data

All six subjects were easily able to perform the task and generate torques at the target level. Figure 2A illustrates raw torque traces for wrist flexion performed by subject PD. Three MVT trials are shown (three highest traces) and six target matching trials at each of the six target levels. MVT, mean force and standard deviation of force were calculated for each muscle of each subject, as described in the "Methods". Though MVT trials were quite long, there was no evidence for a systematic decline in MVT over the three trials as might be expected if subjects were experiencing fatigue. The lower lines in Fig. 2A illustrate 36 target matching trials and show the extent of the slow drift in force due to the lack of visual feedback. This slow drift was removed by filtering before further analysis, and it was confirmed that the amount of drift did not vary between the different muscles.

Figure 2B illustrates the relationship between mean torque and standard deviation of torque for all four tested joints of subject PD. It is clear that the slope of this relationship, i.e. the coefficient of variation (CV), is different for each joint, and is larger for more distal joints. Similar results were found for the other subjects.

To characterise this change in CV fully, the CV of each joint of each subject was plotted against the MVT of that joint in Fig. 3A, and the natural logarithm of the same data is shown in Fig. 3B. A fine line connects the joints studied in each subject, in the left-to-right order: thumb, finger, wrist, elbow. It is clear for most subjects that this line decreases steeply at first and becomes nearly flat as MVT increases, which means that stronger joints generate less variable torques. Linear regression of the natural logarithms of CV and MVT (Fig. 3B) gives the fit parameters c and k in the power law CV=exp(c) MVT^k for each subject, which are summarised in the upper part of Table 2. The mean (range) of k across the six subjects was −0.256 (−0.131 to −0.417), and the mean (range) of c was −3.91 (−3.55 to −4.16). The fit line obtained using these mean values is shown as a grey dashed line in each plot of Fig. 3. To summarise: the main experimental finding is that motor output noise is greater at distal joints acted upon by weaker muscles as demonstrated by the relationship between CV and MVT. The simulations addressed the issue of whether the differences in number of motor units according to muscle strength can account for this relationship.

Muscle simulations

Figure 4A shows the relationship between the number of motor units (MUN) and MVT found from the literature and summarised in Table 1. From the limited data set available, it suggests that muscles with more motor units generate larger torques and this relationship is approximated by a power law. Figure 4B illustrates the relation-
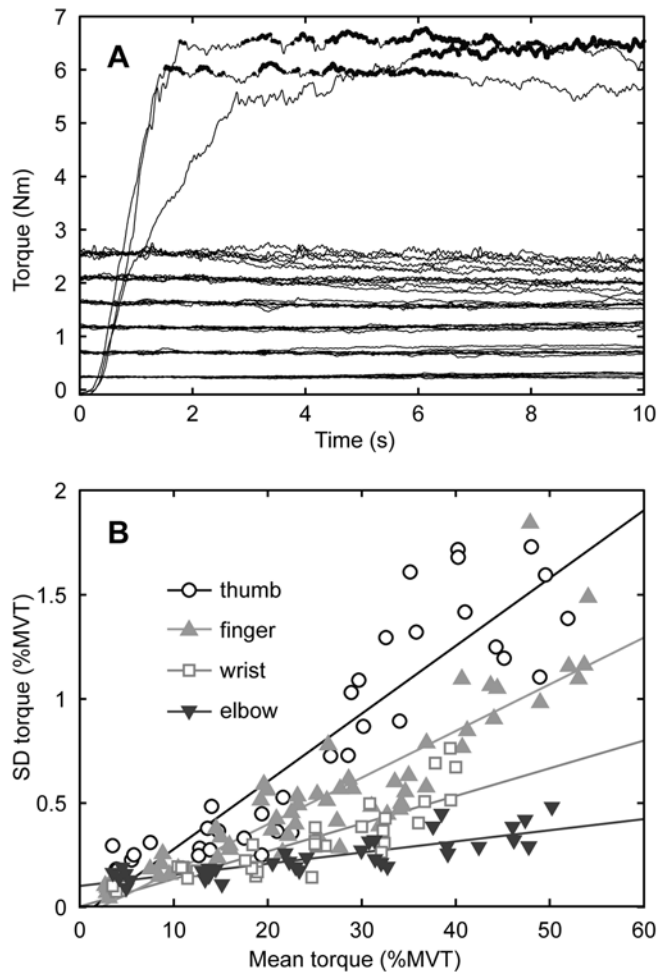
Fig. 2A, B   Torque data from a single subject. A Example torque traces recorded from subject PD during wrist flexion. The *three highest traces* are the three trials when the subject was asked to produce his maximum voluntary contraction, and the *black dots* indicate the 1,000 highest points (i.e. 4 s) on each trace used to calculate the MVT for this joint (6.33 Nm). The *lower traces* are the 36 trials where the subject was asked to match a target torque level; visual feedback was removed 2 s into the trace. B Relationship between mean torque and standard deviation of torque for subject PD, plotted as a percentage of maximum voluntary torque. Thirty-six symbols are plotted for each muscle indicating the mean and standard deviation on each trial. *Solid lines* indicate the linear regression sd = *a* mean + *b* for each muscle; the fit parameters are (*a, b, r²*): thumb: 0.033, −0.047, 0.82; finger 0.022, −0.050, 0.78; wrist: 0.013, 0.002, 0.77; elbow: 0.005, 0.102, 0.69, and all fits were significant at *p*<0.001. The slope parameter *a* gives the coefficient of variation for each muscle
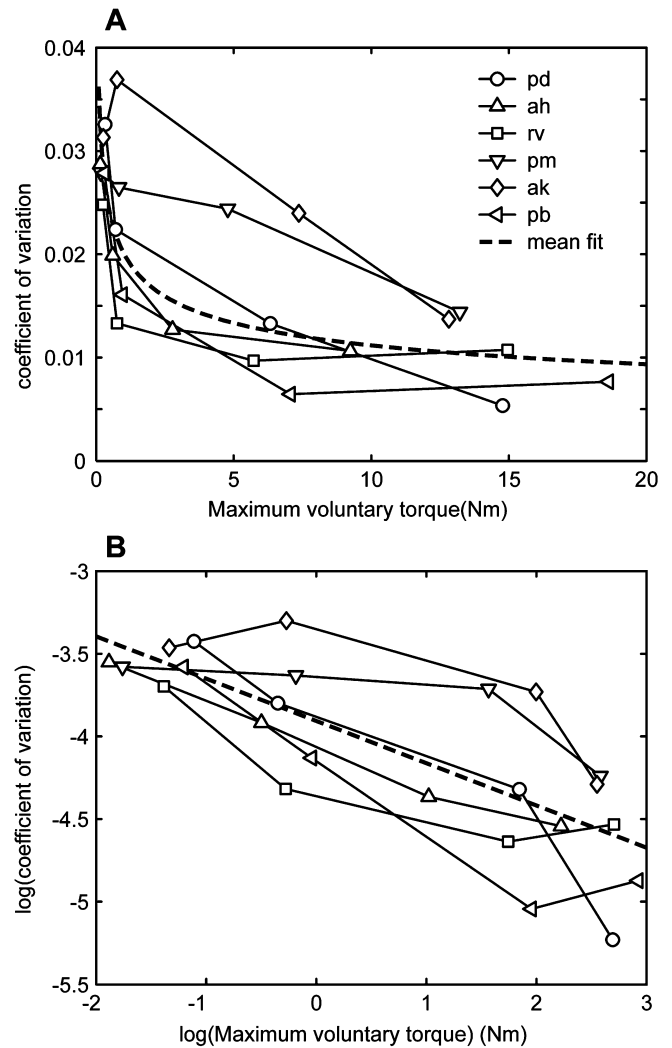

Fig. 3A, B   The relationship between maximum voluntary torque and coefficient of variation for all subjects and all joints. The data is plotted on linear axes in A and the natural log of the same data is plotted in B. The four joints studied in each subject are connected by a *fine line*. In each case, the *leftmost symbol* plots the CV of torque generated by the thumb against the MVT of the thumb, followed by equivalent data for the finger, wrist and elbow in order. Linear regression was performed on the log of the data for each subject, and the average fit over all subjects is shown as a *heavy line* in both plots. The fit parameters for each subject are given in the upper part of Table 2

ship between the number of motor units in each muscle model and the coefficient of variation of force for that muscle for the three sets of simulations with different levels of spike train noise. The regressions for the three sets of simulations have a very similar power (~ −0.5, that is, an inverse square root) but differ in their intercept. This is not surprising because it is known that increasing the level of spike train noise increases the level of output noise (Jones et al. 2002). Using the data in Fig. 4A and B, we calculated the MVT of each simulated muscle and plot it against the CV in Fig. 4C and D. These plots are

equivalent to Fig. 3A, B, and for comparison the mean fit to the experimental data is shown as a dashed line in all these plots. For the simulations, it can be seen that as the MVT increases, the CV decreases, and that the mean of the experimental data falls between the lines for the simulations with 0.2 and 0.4 levels of spike train noise.

The fit parameters *k* and *c* in CV=exp(*c*) MVT^k were calculated for the three simulations and are summarised in the lower part of Table 2. If we compare the parameter values between the subjects and the simulations (upper and lower parts of Table 2), we see that the simulation values of *k* are similar to and lie within the range of *k* for every subject. A *t*-test showed no significant difference between the experimental and simulation values of *k*

Table 2 Parameter estimates for CV=exp(c) MVT^{-k}. Data is given for subjects and simulations (±95% confidence limits), and the parameters obtained for the simulations fall within the parameter range found for the subjects

	k parameter	c parameter
Subject		
pd	−0.417 (±0.40)	−3.87 (±0.69)
ah	−0.249 (±0.09)	−4.04 (±0.14)
rv	−0.197 (±0.33)	−4.16 (±0.59)
pm	−0.131 (±0.28)	−3.72 (±0.48)
ak	−0.196 (±0.40)	−3.55 (±0.69)
pb	−0.343 (±0.35)	−4.09 (±0.66)
Mean	−0.256	−3.91
Simulation		
Spike train noise = 0.2	−0.261 (±0.016)	−4.34 (±0.043)
Spike train noise = 0.4	−0.257 (±0.017)	−3.69 (±0.046)
Spike train noise = 0.6	−0.262 (±0.013)	−3.29 (±0.036)
Mean	−0.260	−3.77

(p=0.947, df=7, t=0.068). The simulation values of c differed across the simulations, covering a similar range to the experimental values, and a t-test showed no significant differences between them (p=0.601, df=7, t=0.547).

Strong and weak muscle simulations

In order to obtain an intuitive understanding of why the noise level varies between muscles, detailed simulations of a strong muscle (320 motor units) and a weak muscle (160 motor units) were performed and the results are illustrated in Fig. 5. Figure 5A illustrates torque traces generated by two simulations, and it is clear that for a similar torque output, the strong muscle (black traces) is less variable than the weak muscle (grey traces). Figure 5B shows the firing rate of every fifth motor unit that generated the traces plotted in Fig. 5A. The weak muscle has fewer units firing and higher firing rates than the strong muscle, even though the weak muscle has not activated every unit. It is widely believed that lower firing rates, where twitches are less fused, will lead to higher force variability. This is true for muscle fibres stimulated electrically at constant frequency (for example, Westling et al. 1990) and has also been shown for single twitches as measured by spike triggered averaging (Calancie and Bawa 1986). However, these studies do not take into account the slow fluctuations in force output which occur in response to realistically noisy spike trains. These slow fluctuations (illustrated in Jones et al. 2002, Fig. 4A) are not time locked to individual spikes, but are due to the overall spike train

Fig. 4A–D Simulation results. **A** The relationship between the number of motor units and maximum voluntary torque obtained from the literature (Table 1). The fit line has an r^2 of 0.67 and a p<0.02. **B** The relationship between the number of motor units and the coefficient of variation obtained from the simulation. Results for three sets of simulations with different levels of input noise, as specified in the legend of plot **C**. The equations of each fit line are given. **C** The relationship between maximum voluntary torque and coefficient of variation obtained from the simulation results when scaled according to the data from the literature. Results are shown for three sets of simulations with different levels of input noise and for comparison the mean fit to the experimental data from Fig. 3A is shown as a *dashed line*. The fit parameters for each simulation are given in the lower part of Table 2. **D** The logarithm of the data in **C**
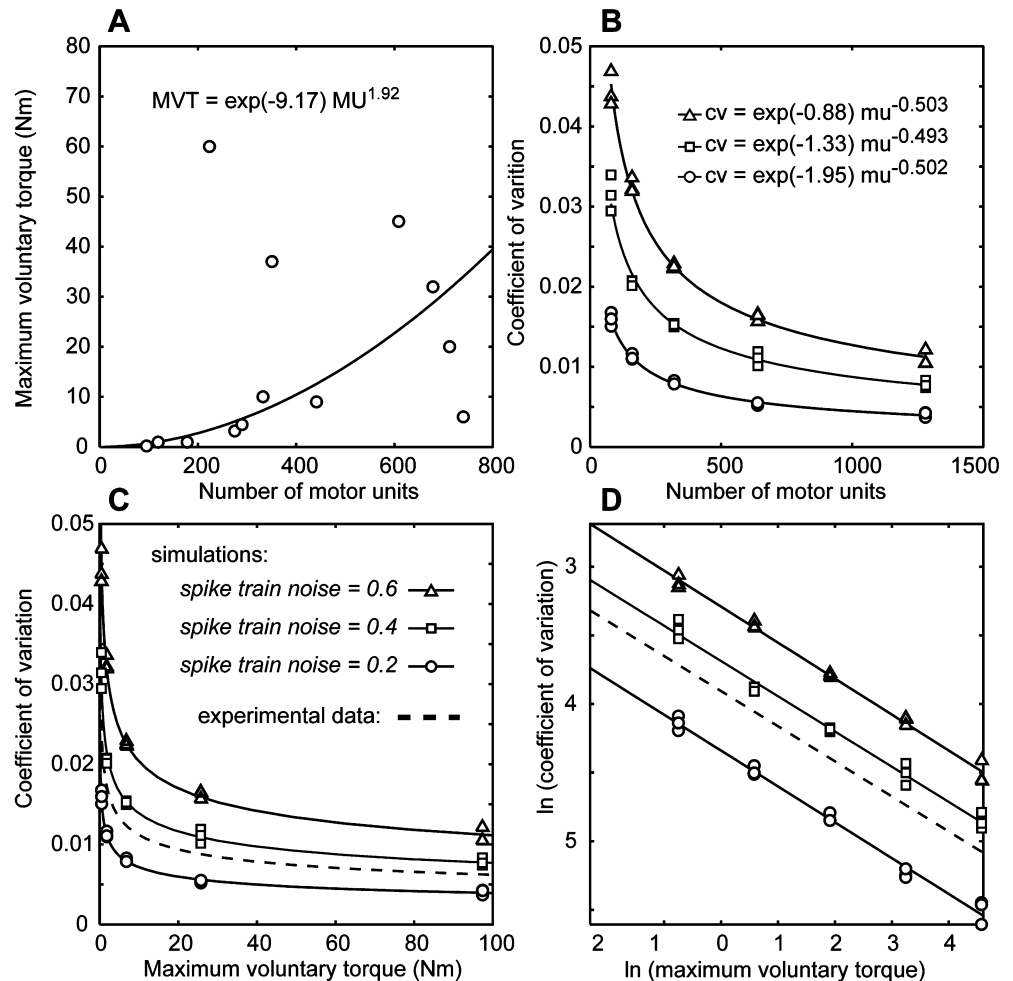
variability. When motor unit noise is measured over a period of seconds, slow fluctuations contribute greatly to the noise, and force variability is seen to increase in a square-root relation with mean force output as the firing rate increases. Thus, the weak muscle with higher firing rates should be expected to be more noisy, as is observed in Fig. 5A.

Figure 5C examines this effect across the whole output range of the muscle, illustrating the number of motor units recruited at a particular output torque. The strong muscle (black) has more units active across most of the range, but the magnified inset shows that the weak muscle has more active units for torques between 0 and 0.058 Nm, which is 3.2% of the weak muscle's torque range. Figure 5D confirms that the coefficient of variation of torque, i.e. the slope of the line, generated by the strong muscle is lower than that generated by the weak muscle, and is comparable to the experimental data shown in Fig. 2B. Note that towards the bottom of the range, the data points from both muscles overlap. Here, the lower firing rate of the strong muscle will act to decrease its noise, while the low number of units firing will act to increase it, leading to a very similar noise level across the strong and weak muscles.

The coefficient of variation for both simulated muscles over the force range is plotted in Fig. 5E, which illustrates that the CV increases at very low forces, observed experimentally by Galganski et al. (1993) and Enoka et al. (1999). The impact of changing recruitment is shown in Fig. 5F. Even though recruitment was varied from none (rate coding only) to a 100-fold range of thresholds, there was no appreciable change in CV. This suggests that differences in recruitment strategy between muscles are not an important factor in differences in noise level between muscles.

Discussion

We have demonstrated how joint strength and motor unit number influence the variability of joint torque. As joint strength (MVT) increases, the coefficient of variation of joint torque (CV) decreases in an exponential fashion for human subjects. Since CV is a dimensionless measure, it is the same whether is it calculated based on %MVT, absolute torque or force produced at any point along the effector. As the experiments were performed under isometric conditions, factors such as damping due to inertial differences at the four joints are irrelevant. The simulations were able to accurately model the experimental data, and show that CV is dependent on the number of motor units innervating each muscle (MUN) according to an inverse square root power law. Therefore we conclude that stronger muscles with more motor units have a lower coefficient of variation of torque than weaker
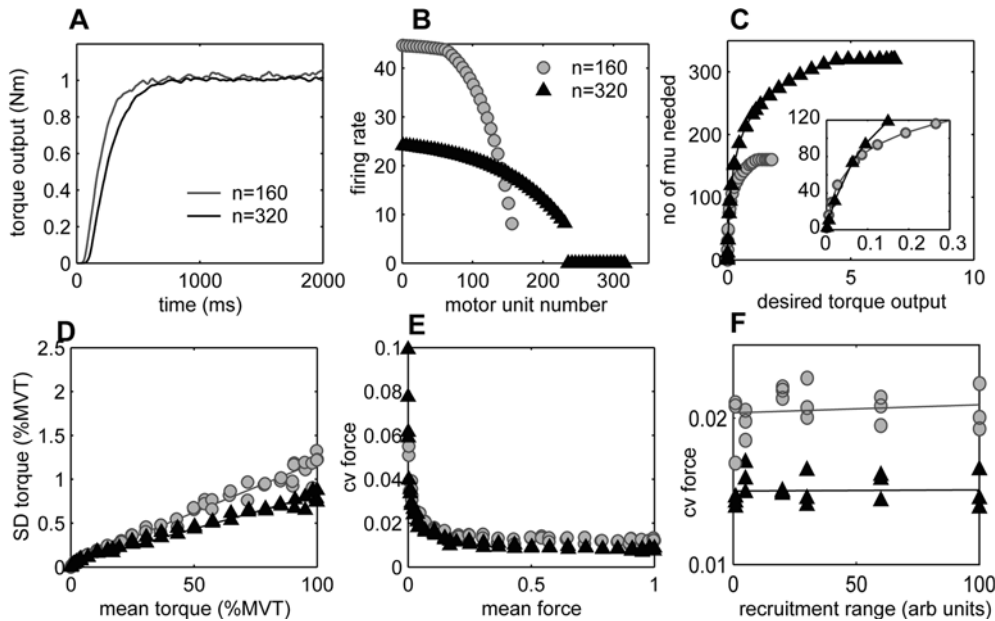

Fig. 5A–F Simulation of a weak and strong muscle. **A** Torque traces produced by a weak muscle (*black*, 160 motor units, MVT=1.79) and a strong muscle (*grey*, 320 motor units, MVT=6.79 Nm) generating 1 Nm of torque. This is 56% MVT for the weak muscle and 14% MVT for the strong muscle. **B** The number of motor units active and firing rates in each muscle when generating the traces shown in **A**. Every 5th motor unit is shown for clarity. The weak muscle has fewer units firing and at higher firing rates than the strong muscle. **C** The number of active motor units over the torque range of each muscle. The *inset* shows an enlargement of the bottom of the scale. The strong muscle has more active units at all torque levels above 0.058 Nm. **D** The relation between mean torque and standard deviation of torque for the strong and weak muscle. The strong muscle is less noisy across the whole torque range. The parameters of the linear regression sd = a mean + b for each muscle in order a, b, r^2 are: strong: 0.0150, 0.0300, 0.98; weak: 0.0211, 0.0305, 0.98. Parameter a is the coefficient of variation for each muscle. **E** The relation between mean force and coefficient of variation of force for a strong and weak muscle. In both cases, CV is greater for the bottom 5% of the force range, as observed experimentally. **F** The influence of recruitment on motor noise. One hundred fold changes in the range of recruitment thresholds have no effect on the level of noise produced by either the small or large muscles

muscles with fewer motor units. This means that a strong muscle will generate a target torque level with less variability than a weaker muscle.

Why does motor noise vary across muscles?

The experimental data presented here demonstrate that muscle noise decreases as muscle strength increases, and the simulation data demonstrate that muscle noise decreases as motor unit number increases. Together the results are compatible with the hypothesis that muscle noise falls as muscle strength increases because stronger muscles have more motor units. However, we can consider other possible sources that could contribute to the different levels of noise between muscles. Five possible sources of motor noise are: (1) central control signals, (2) range of motor unit recruitment, (3) motor unit synchrony, (4) spike train noise, and (5) number of motor units. Which of these possible sources is most likely responsible for the change in force variability between muscles we have observed?

Differences in central control are unlikely to account for the observed data because larger cortical areas, and therefore presumably a greater resolution, are available for the control of small muscles such as the fingers than for larger muscles in the upper arm (Penfield and Rasmussen 1950), but the noise followed the opposite pattern. Moreover, the changes in force noise did not arise from differences in the visual control of the force because visual feedback was identical in terms of scaling on the screen, and no feedback was given during the period when force variability was recorded. Thus differences in visual or central signals cannot account for the increase in muscle noise with decreased muscle size.

The range of motor unit recruitment has previously been shown to have important effects on the linearity of noise output (Jones et al. 2002). Furthermore, muscles of different sizes are known to have different recruitment ranges, which might influence their force variability. However, as Fig. 5F (and Taylor et al. 2003) demonstrate, changing the recruitment range in simulations did not have a significant impact on the CV of muscle force, so this factor is unlikely to contribute to the variation in noise observed. These simulations confirm that the imperfect assumption of equal recruitment patterns across all muscles made in the modelling cannot adversely affect the conclusions drawn from the model, because the same noise level would be obtained from each muscle whatever its recruitment strategy.

Differences in synchrony between muscles could have an impact on motor noise and there is empirical evidence for greater synchronization in smaller distal muscles. Datta and Stephens (1990) report that synchronization of motor units in normal subjects is greater in first dorsal interosseous (FDI) than in tibialis anterior (TA). Since increased synchronization leads to increased noise (Yao et al. 2000; Taylor et al. 2003), this would result in greater noise in the small distal FDI compared to the larger TA muscle. It has been shown that changes within the physiological range of synchrony can double force CV (Yao et al. 2000), but our empirical data show that the change in CV from the elbow to the thumb is on average 3.5-fold over all the subjects. This suggests that changes in synchrony between different muscles may contribute but could not alone account for the changes in CV observed in the muscles of the arm.

Spike train noise, measured as the variability of motor neuron firing rates or interspike intervals (ISIs), is also known to affect force output variability, but there is no evidence that it changes systematically across muscles. Nordstrom and Miles (1991) found a range of coefficients of variation for motor neuron ISIs from 0.18 to 0.47 over 37 units from human masseter, and the values reported for other muscles tend to also fall within this range (Tanji and Kato 1973; Bigland-Ritchie et al. 1983; Garland et al. 1994; Semmler and Nordstrom 1998; Luschei et al. 1999; Macefield et al. 2000) with no clear ordering of the spike train noise with muscle size. Changes in spike train noise between muscles are therefore unlikely to be responsible for the observed changes in force variability.

Our simulations have shown that the difference in motor unit number between muscles is a plausible and, in the model, a sufficient cause of the difference in force variability between muscles. We now consider why differences in motor unit number between muscles lead to differences in motor noise, with reference to the detailed simulations of a strong and weak muscle. Figure 5 demonstrates that over 97% of the output range of the weak muscle, the strong muscle has more motor units active and lower firing rates than the weak muscle, leading to less force noise. We have previously shown that the standard deviation of force output increases with increased motor neuronal firing rates and increased mean force (Jones et al. 2002; Fig. 4C). Therefore, both the higher firing rates and fewer active units in the weak muscle compared to the strong muscle lead to a more variable output for a given mean level of force. This relationship between force noise and the number of active motor units was independently predicted in a recent simulation study (Taylor et al. 2003).

The counterintuitive finding that the strong muscle has more active units to produce a given force level is due to the unequal distribution of force output and firing thresholds across the motor neuron pool. The motor neuron pool is made up of many units with a low threshold and small twitch force, and fewer units with a high threshold and large twitch force (Hennemann 1957; Gustafsson and Pinter 1984; Powers and Binder 1985), which are recruited in an orderly fashion from smallest to largest. Our simulation used the same distribution of motor unit thresholds as Fuglevand et al. (1993), that is, an exponential distribution in which the last unit recruited has a recruitment threshold 30 times greater than the first unit. Though changing the distribution of thresholds might influence the noise level found in the simulations, it is likely that a dramatic and unrealistic change would be required for strong muscles to produce as much noise as or more noise than weak muscles.

These detailed simulations make it clear that changing the number of motor units between muscles must lead to changes in their motor noise. Since MUN is known to change systematically with muscle size and MVT, we suggest that changes in MUN can fully account for the experimentally observed changes in CV. The number of motor units in a muscle in effect places a 'lower bound' on the level of motor noise in that muscle, and additional factors such as synchrony and inaccurate central control can only increase the noise above this level. This MUN explanation of motor noise has good explanatory power as the primary cause of differences in output noise between muscles, and makes several predictions for further experiments, some of which are discussed below.

Implications of the simulation results

The discovery of a close systematic relation between the number of motor units and the level of noise produced by a muscle (Fig. 4B) has several important implications for our understanding of the sources of variability in human movement. It is known that number of motor units innervating each muscle does not change from birth to adulthood in healthy subjects (Montgomery 1962; Tomlinson and Irving 1977). This means that the level of motor noise due to the number of motor units will also remain constant over a lifetime in healthy subjects. Thus improvements in accuracy observed over childhood should be due to other factors such as synchrony, spike train variability or the variability in generating central motor commands (Deutsch and Newell 2001). Within the adult, manipulations such as exercise should not be expected to alter the level of noise in a muscle (Keen et al. 1994; Semmler and Nordstrom 1998). Interestingly, Keen et al. (1994) also reported that force variability was reduced by strength training in elderly subjects, suggesting that the increase in variability observed in this population cannot be due solely to the loss of motor units. This position is supported by recent simulations (Enoka et al. 2003), which suggest that increased force variability in the elderly is not primarily due to loss of motor units. In contrast, it is likely that diseases which involve motor unit loss, in particular amyotrophic lateral sclerosis/motor neuron disease, should also lead to an increase in force variability, independent of the progressive decline in muscle strength (Bromberg et al. 1993; Bromberg and Larson 1996). Though changes in force variability have not, to our knowledge, been tested in this patient group, they are clearly predicted by the results presented here, and could have implications for accurate movements in daily life in this patient group.

Changes in CV with MUN also have the potential to contribute to our understanding of how CV changes over the force range within a single muscle. It has been shown that the coefficient of variation of muscle force increases for very low force levels (Galganski et al. 1993; Laidlaw et al. 2000; Schiffman and Luchies 2001; Taylor et al. 2003), and this behaviour is also seen in the simulation (Fig. 5F).

At the lowest force levels, fewer motor units are active in the muscle (Fig. 5C), and thus force output should be expected to show a higher coefficient of variation, as is observed. This suggests that there is a link between the number of active motor units and force CV within a single muscle, similar to the relation between total MUN and force CV between muscles. However, the exact nature of this link at the single muscle level remains to be tested in detail.

The CV-MUN relationship also has implications for our interpretation of the experimental data collected in this study. We experimentally measured the coefficient of variation of joint torque and the maximum voluntary torque produced at four joints, and used these results to draw conclusions about the distribution of noise in the muscles of the arm. Although the torque produced at a joint is not the same as the force produced in each muscle, torques produced by several agonist muscles will sum linearly. Furthermore, the simulation results suggest that the coefficient of variation of force generated by two muscles with, say, 100 units, will be the same as the CV of force generated by one muscle with 200 units, because the total number of units is the critical factor in determining the noise. Thus we can be confident that the experimental results can be generalised from the case of torque and torque variability to the underlying muscle force and force variability, taking muscle moment arms into account, without introducing inaccuracies.

The equations predicting muscle parameters

Three quantitative relationships have been suggested that link three muscle parameters: the coefficient of variation of muscle torque (CV), the number of motor units innervating a muscle (MUN) and the maximum voluntary torque produced by a muscle (MVT). These three relationships arise from simulation (CV $\propto$ MUN$^{-0.5}$), experiments (CV $\propto$ MVT$^{-0.25}$) and a literature review (MVT $\propto$ MUN$^{1.92}$). Not all of these values are easy to measure in human subjects, so it is useful to consider the accuracy of predictions that could be made using these formulae, both at a general level and for individuals.

The most robust result is the simulation result relating MUN to CV according to:

$$CV = \exp(d)MUN^{-0.5} \qquad (5)$$

where d varied from -1.95 to -0.89 and the power of -0.5 was reliable across all simulations. d is related to the level of spike train noise in the model, which is a free parameter known to vary between individuals (Nordstrom and Miles 1991). So long as d is not a function of MUN, the relation between CV and MUN will hold. Due to the physiological variability of motor neuron spike trains, it would not be possible simply to calculate MUN from a measure of CV, but knowing the relationship between muscle noise and

motor unit number can still contribute to our understanding of the control of movements.

The experimental result related the coefficient of variation of torque (CV) produced at a joint to the strength of the joint (MVT). Both CV and MVT change through an individual's lifespan (for example, Connolly 1970; Laidlaw et al. 2000; Deutsch and Newell 2001), and MVT can be greatly affected by exercise or training. Thus any predictions could not be generalised beyond a particular population, in this case the healthy young adults who were subjects for this study. Within this population, muscle strength, motor unit number and spike train noise can be assumed to vary, and without evidence of a systematic relation between these factors at the level of individuals it would not be sensible to predict an individual's MUN based on their MVT or CV. However, the parameter fits found over six subjects did not differ greatly (see Table 2) and can be considered to be robust for the population. Thus the experimental finding that $CV = \exp(-2.76)$ $MVT^{-0.25}$ can be useful for understanding and building general models of the role of noise in motor control.

Values from a range of sources in the literature were used to obtain the third relationship, $MVT = \exp(-9.17)$ $MUN^{1.92}$. As data was available for only 13 muscles from a number of sources, this equation should be considered as an approximation only. The MUN data in particular has several possible sources of inaccuracy, as the major anatomical study which provided five data points was conducted on a single subject (Feinstein et al. 1955), while the electrophysiological studies find a range of values between individuals (Stein and Yang 1990; McComas 1998; Chan et al. 2001). It is interesting to note that the largest outlier in Fig. 4A is the data point for vastus medialis, where the MUN was determined electrophysiologically, and these methods are known to be susceptible to underestimation (McComas 1998), while the MUN of the next outlier (Sartorius in the lower right of Fig. 4 A) was determined by postmortem counting, which is potentially susceptible to overestimation due to motor unit branching (Eccles and Sherrington 1930). If such plausible sources of error were present in these MUN counts, the true value for these outliers would be closer to the fitted curve. Further data on motor unit counts in these and other muscles would be highly valuable in confirming the relationship between muscle strength or size and motor unit number, and in determining which muscles are exceptions to the rule and why. For example, the muscles controlling the eyes are known to have a very high number of motor units for their size (Buchthal and Schmalbruch 1980), which might be expected if the eyes require exceptionally high accuracy, and thus low noise in their muscle force.

Despite the possible sources of variability, the relationships found from the experiment, simulations and literature survey were all reliable and can be useful in understanding the control of the arm. Interestingly, it is possible to derive any one of these three relationships from the other two. For example, equating $CV = \exp(-2.76)$ $MVT^{-0.25} = \exp(d)MUN^{-0.5}$, we can simplify to obtain

$MVT = \exp(4d - 11.04)$ MUN^2. The power of 2 on the MUN term falls within the confidence limits of the power term calculated from the literature (power = 1.92, 95% confidence limits 0.74–3.11). This confirms the validity of the three power laws as defining the overall relationship between MUN, CV and MVT. It is important also to realise that of the three correlations described above, it is only the MUN-CV relationship which we believe to be causative, that is, the number of motor units innervating a muscle determines the coefficient of variation of muscle force. In contrast, the relations between CV and MVT or MUN and MVT are likely to be a corollary of the structure of the muscle-nerve system, and the question of whether, for example, MUN might relate more closely to maximum muscle force than MVT, remains open.

Optimal muscle co-ordination

Understanding the distribution of noise in the arm has implications for our understanding of the control of the arm. The human arm has approximately 30 muscles to control 7 joint degrees of freedom from the shoulder to the wrist, excluding the translation degrees of freedom of the shoulder/scapula system. This redundancy means that every movement must involve selecting one of all the possible muscle activation patterns that would achieve the desired torque at each joint. Many different principles have been suggested for selecting the distribution of forces between several muscles, but most optimise some function of muscle force (*f*) and physiological cross sectional area (PCSA). In a comparison of several possible cost functions with experimental data, van Bolhuis and Gielen (1999) concluded that muscles should be activated to minimise the sum of muscle stress squared, and Gomi (2000) reached the same conclusion independently. The cost function they propose is:

$$C_{\text{stress}} = \sum_{i=1}^{n} (f_i/\text{PCSA}_i)^2 \qquad (6)$$

where *n* is the number of muscles involved in the task, and subject to the constraint:

$$F = \sum_{i=1}^{n} f_i \qquad (7)$$

where *F* is the total force required.

In contrast, the TOPS model (Harris and Wolpert 1998) proposes that muscles should be activated to minimise the effects of muscle noise, i.e.

$$C_{\text{TOPS}} = \sum_{i=1}^{n} \sigma_i^2 \qquad (8)$$

where σ^2 is the variance of force produced by each muscle.

In order to apply this cost function to specific muscle groups, we can derive a new cost in terms of the number of motor units in each muscle involved in the task (see "Appendix" for derivation):

$$C_{\text{TOPS}} = \sum_{i=1}^{n} (f_i^2 / \text{MUN}_i) \qquad (9)$$

This gives a precise method to calculate the optimal muscle activation pattern under TOPS, and because MUN does not change from birth to adulthood (Montgomery 1962) and is not influenced by exercise or training, this is a robust and general cost applicable to a range of situations. In simple terms, this cost function means that in a synergistic group, muscles with more motor units should be activated in preference to those with fewer motor units, because this should lead to the least noise in the total force output. This is in agreement with the patterns of muscle activation found by Hunter et al. (2002), who found greater normalised EMG in brachialis (MVT=13.3, calculated MUN=456) than in biceps (MUN=440) or brachioradialis (MUN=333) in a submaximal contraction. However, this must be interpreted with caution, as the normalised EMG is an indirect measure of the force produced by each muscle. It is more helpful to assess the validity of muscle cost functions by examination of muscle preferred directions (van Bolhuis and Gielen 1999; Gomi 2000). The validity of this TOPS cost could be also confirmed if muscle use patterns were shown not to change with strength training, a manipulation which changes muscle size and strength, but not motor unit number or muscle noise (Keen et al. 1994). If the TOPS cost is able to account for human muscle activation patterns, this will be further evidence that the reduction of the consequences of signal-dependent noise is an overall principle for the control of human movement.

Overall conclusion

We have demonstrated that stronger more proximal joints in the human arm have lower levels of motor noise than weaker more distal joints, and that there is a systematic relationship between joint strength and noise. We have also shown that the level of noise found in muscles is systematically related to the number of motor units in each muscle. This suggests that motor noise follows a similar distribution in the arm to proprioceptive noise and that change in the size or strength of arm muscles should not change the variability of muscle force. Using these results, we have derived a new cost function that describes how muscles in the arm should be activated to minimise the consequences of signal-dependent noise under the TOPS framework.

Appendix

Two cost functions describing how muscles should be used to minimise the consequences of signal-dependent noise can be derived from the basic TOPS cost function given in Eq. 8. Using the simulation results given in Eq. 5 and substituting:

$$CV = \sigma / f \qquad (10)$$

gives:

$$\sigma = \exp(d) f \, \text{MUN}^{-0.5} \qquad (11)$$

As this holds for every muscle, the constant $\exp(d)$ can be ignored and σ can be substituted into the TOPS cost function (Eq. 8) to give:

$$C_{\text{TOPS}} = \sum_{i=1}^{n} (f_i^2 / \text{MUN}_i) \qquad (12)$$

Despite the interesting predictions of the MUN cost function, the current paucity of data on motor unit numbers means that this cost function is not easy to apply in practice. For this reason, we also derive a second, more practical cost function, based on the experimental results. Taking the mean parameters for the six subjects, we have shown that:

$$CV = \exp(-2.76) \text{MVT}^{-0.25} \qquad (13)$$

Substituting Eq. 10 gives:

$$\sigma = \exp(-2.76) f \, \text{MVT}^{-0.25} \qquad (14)$$

Again, the constant $\exp(-2.76)$ can be ignored and σ can be substituted into Eq. 8 to give:

$$C_{\text{TOPS}} = \sum_{i=1}^{n} (f_i^2 / \text{MVT}_i^{0.5}) \qquad (15)$$

This cost function can be used to determine the optimal control strategy for minimising noise over multiple muscles and requires only knowledge of the maximum voluntary torque produced by each muscle, which is available in standard tables (for example, Winters and Stark 1988).

References

Abend W, Bizzi E, Morasso P (1982) Human arm trajectory formation. Brain 105:331–348

An KN, Hui FC, Morrey BF, Linscheid RL, Chao EY (1981) Muscles across the elbow joint: a biomechanical analysis. J Biomech 14:659–669

Basmajian JV (1978) Muscles alive: their functions revealed by electromyography. Williams & Wilkins, Baltimore

Basmajian JV, Latif A (1957) Integrated actions and functions of the chief flexors of the elbow: a detailed electromyographic study. J. Bone Int Surg 39A:1106–1118

Bigland-Ritchie B, Johansson R, Lippold OC, Smith S, Woods JJ (1983) Changes in motoneurone firing rates during sustained maximal voluntary contractions. J Physiol 340:335–346

Brand PW (1985) Clinical mechanics of the hand. CV Mosby Co., St. Louis

Brochier T, Spinks R, Umilta MA, Kirkwood PA, Lemon RN (2001) Specificity of muscular activation during skilled grasp of different objects in monkeys. Soc Neurosci Abstr:303.8

Bromberg MB, Larson WL (1996) Relationships between motor-unit number estimates and isometric strength in distal muscles in ALS/MND. J Neurol Sci 139 Suppl:38–42

Bromberg MB, Forshew DA, Nau KL, Bromberg J, Simmons Z, Fries TJ (1993) Motor unit number estimation, isometric strength, and electromyographic measures in amyotrophic lateral sclerosis. Muscle Nerve 16:1213–1219

Buchanan TS, Moniz MJ, Dewald JP, Zev Rymer W (1993) Estimation of muscle forces about the wrist joint during isometric tasks using an EMG coefficient method. J Biomech 26:547–560

Buchthal F, Schmalbruch H (1980) Motor unit of mammalian muscle. Physiol Rev 60:90–142

Calancie B, Bawa P (1986) Limitations of the spike-triggered averaging technique. Muscle Nerve 9:78–83

Chan KM, Doherty TJ, Brown WF (2001) Contractile properties of human motor units in health, aging, and disease. Muscle Nerve 24:1113–1133

Chao EY, An KN, Cooney WP, Linscheid RL (1989) Biomechanics of the hand; a basic research study. World Scientific, Singapore

Christensen E (1959) Topography of terminal motor innervation in striated muscles from stillborn infants. Am J Phys Med 38:17–30

Collins JJ (1995) The redundant nature of locomotor optimization laws. J Biomech 28:251–267

Connolly K (1970) Mechanisms of motor skill development. Academic Press, London

Crowninshield RD, Brand RA (1981) A physiologically based criterion of muscle force prediction in locomotion. J Biomech 14:793–801

Datta AK, Stephens JA (1990) Synchronization of motor unit activity during voluntary contraction in man. J Physiol 422:397–419

de Carvalho VC (1976) Study of motor units and arrangement of myons of human musculus plantaris. Acta Anatomica 96:444–448

Deutsch KM, Newell KM (2001) Age differences in noise and variability of isometric force production. J Exp Child Psychol 80:392–408

Dul J, Johnson GE, Shiavi R, Townsend MA (1984a) Muscular synergism—II. A minimum-fatigue criterion for load sharing between synergistic muscles. J Biomech 17:675–684

Dul J, Townsend MA, Shiavi R, Johnson GE (1984b) Muscular synergism—I. On criteria for load sharing between synergistic muscles. J Biomech 17:663–673

Eccles JC, Sherrington CS (1930) Numbers and contraction-values of individual motor units examined in some muscles of the limb. Proc R Soc Lond B Biol Sci 106:326–357

Enoka RM, Burnett RA, Graves AE, Kornatz KW, Laidlaw DH (1999) Task- and age-dependent variations in steadiness. Prog Brain Res 123:389–395

Enoka RM, Christou EA, Hunter SK, Kornatz KW, Semmler JG, Taylor AM, Tracy BL (2003) Mechanisms that contribute to differences in motor performance between young and old adults. J Electromyogr Kinesiol 13:1–12

Fagg AH, Shah A, Barto AG (2002) A computational model of muscle recruitment for wrist movements. J Neurophysiol 88:3348–3358

Feinstein B, Lindegard B, Nyman E, Wohlfart G (1955) Morphological studies of motor units in normal human muscles. Acta Anatomica 23:127–142

Fitts PM (1954) The information capacity of the human motor system in controlling the amplitude of movement. J Exp Psychol 47:381–391

Flanders M, Soechting JF (1990) Arm muscle activation for static forces in three-dimensional space. J Neurophysiol 64:1818–1837

Fuglevand AJ, Winter DA, Patla AE (1993) Models of recruitment and rate coding organization in motor-unit pools. J Neurophysiol 70:2470–2488

Galganski ME, Fuglevand AJ, Enoka RM (1993) Reduced control of motor output in a human hand muscle of elderly subjects during submaximal contractions. J Neurophysiol 69:2108–2115

Garland SJ, Enoka RM, Serrano LP, Robinson GA (1994) Behavior of motor units in human biceps brachii during a submaximal fatiguing contraction. J Appl Physiol 76:2411–2419

Gomi H (2000) Minimum principles for muscle-coordination evaluated by the directional preference of muscle activation during multijoint-arm force regulation task. Tech Rep of IEICE, NC2000–10, pp 9–16

Gustafsson B, Pinter MJ (1984) An investigation of threshold properties among cat spinal alpha-motoneurones. J Physiol 357:453–483

Hall LA, McCloskey DI (1983) Detections of movements imposed on finger, elbow and shoulder joints. J Physiol 335:519–533

Hamilton AFdC, Wolpert DM (2002) Controlling the statistics of action: obstacle avoidance. J Neurophysiol 87:2434–2440

Harris CM, Wolpert DM (1998) Signal-dependent noise determines motor planning. Nature 394:780–784

Hennemann E (1957) Relation between size of neurons and their susceptibility to discharge. Science 126:1345–1347

Henneman E, Somjen G, Carpenter DO (1965) Excitability and inhibitability of motoneurons of different sizes. J Neurophysiol 28:599–620

Hoffman DS, Strick PL (1999) Step-tracking movements of the wrist. IV. Muscle activity associated with movements in different directions. J Neurophysiol 81:319–333

Hunter SK, Ryan DL, Ortega JD, Enoka RM (2002) Task differences with the same load torque alter the endurance time of submaximal fatiguing contractions in humans. J Neurophysiol 88:3087–3096

Jones KE, Hamilton AFdC, Wolpert DM (2002) Sources of signal-dependent noise during isometric force production. J Neurophysiol 88:1533–1544

Keen DA, Yue GH, Enoka RM (1994) Training-related enhancement in the control of motor output in elderly humans. J Appl Physiol 77:2648–2658

Kuwabara S, Mizobuchi K, Ogawara K, Hattori T (1999) Dissociated small hand muscle involvement in amyotrophic lateral sclerosis detected by motor unit number estimates. Muscle Nerve 22:870–873

Laidlaw DH, Bilodeau M, Enoka RM (2000) Steadiness is reduced and motor unit discharge is more variable in old adults. Muscle Nerve 23:600–612

Luschei ES, Ramig LO, Baker KL, Smith ME (1999) Discharge characteristics of laryngeal single motor units during phonation in young and older adults and in persons with Parkinson disease. J Neurophysiol 81:2131–2139

MacConaill MA (1967) The ergonomic aspects of articular mechanisms. In: Evans FG (ed) Studies of the anatomy and function of bones and joints. Springer, Berlin, pp 69–80

Macefield VG, Fuglevand AJ, Howell JN, Bigland-Ritchie B (2000) Discharge behaviour of single motor units during maximal voluntary contractions of a human toe extensor. J Physiol 528:227–234

McComas AJ (1998) 1998 ISEK congress keynote lecture: motor units: how many, how large, what kind? International Society of Electrophysiology and Kinesiology. J Electromyogr Kinesiol 8:391–402

Montgomery RD (1962) Growth of human striated muscle. Nature 195:194–195

Morasso P (1981) Spatial control of arm movements. Exp Brain Res 42:223–227

Nordstrom MA, Miles TS (1991) Discharge variability and physiological properties of human masseter motor units. Brain Res 541:50–56

Pedotti A, Krishnan VV, Stark L (1978) Optimization of muscle-force sequencing in human locomotion. Math Biosci 38:57–76

Penfield W, Rasmussen T (1950) The cerebral cortex of man; a clinical study of localization of function. Macmillan, Oxford

Powers RK, Binder MD (1985) Distribution of oligosynaptic group I input to the cat medial gastrocnemius motoneuron pool. J Neurophysiol 53:497–517

Refshauge KM, Chan R, Taylor JL, McCloskey DI (1995) Detection of movements imposed on human hip, knee, ankle and toe joints. J Physiol 488:231–241

Schiffman JM, Luchies CW (2001) The effects of motion on force control abilities. Clin Biomech (Bristol, Avon) 16:505–513

Schmidt RA, Zelaznik H, Hawkins B, Frank JS, Quinn JTJ (1979) Motor-output variability: a theory for the accuracy of rapid motor acts. Psychol Rev 47:415–451

Semmler JG, Nordstrom MA (1998) Motor unit discharge and force tremor in skill- and strength-trained individuals. Exp Brain Res 119:27–38

Somjen G, Carpenter DO, Henneman E (1965) Responses of motoneurons of different sizes to graded stimulation of supraspinal centers of the brain. J Neurophysiol 28:958–965

Stein RB, Yang JF (1990) Methods for estimating the number of motor units in human muscles. Ann Neurol 28:487–495

Tanji J, Kato M (1973) Firing rate of individual motor units in voluntary contraction of abductor digiti minimi muscle in man. Exp Neurol 40:771–783

Taylor AM, Christou EA, Enoka RM (2003) Multiple features of motor-unit activity influence force fluctuations during isometric contractions. J Neurophysiol 90:1350–1361

Tomlinson BE, Irving D (1977) The numbers of limb motor neurons in the human lumbosacral cord throughout life. J Neurol Sci 34:213–219

Valero-Cuevas FJ, Zajac FE, Burgar CG (1998) Large index-fingertip forces are produced by subject-independent patterns of muscle excitation. J Biomech 31:693–703

van Bolhuis BM, Gielen CC (1997) The relative activation of elbow-flexor muscles in isometric flexion and in flexion/extension movements. J Biomech 30:803–811

van Bolhuis BM, Gielen CC (1999) A comparison of models explaining muscle activation patterns for isometric contractions. Biol Cybern 81:249–261

van Zuylen EJ, Gielen CC, Denier van der Gon JJ (1988) Coordination and inhomogeneous activation of human arm muscles during isometric torques. J Neurophysiol 60:1523–1548

Vasavada AN, Peterson BW, Delp SL (2002) Three-dimensional spatial tuning of neck muscle activation in humans. Exp Brain Res 147:437–448

Westling G, Johansson RS, Thomas CK, Bigland-Ritchie B (1990) Measurement of contractile and electrical properties of single human thenar motor units in response to intraneural motor-axon stimulation. J Neurophysiol 64:1331–1338

Winters JM, Stark L (1988) Estimated mechanical properties of synergistic muscles involved in movements of a variety of human joints. J Biomech 21:1027–1041

Yao W, Fuglevand RJ, Enoka RM (2000) Motor-unit synchronization increases EMG amplitude and decreases force steadiness of simulated contractions. J Neurophysiol 83:441–452

Yeo BP (1976) Investigations concerning the principle of minimal total muscular force. J Biomech 9:413–416