

Dependence of EMG Responses Evoked by Imposed Wrist Displacements on Pre-existing Activity in the Stretched Muscles

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ABSTRACT: The relationship between the segmented EMG activity in flexor carpi radialis evoked by imposed angular wrist displacement was studied with respect to the level of pre-existing background activity in 30 normal human subjects. Input-output response planes demonstrate that the magnitude of the M1 & M2-3 segments is dependent on both the displacement parameters and the level of pre-existing EMG activity in the stretched muscle. If the level of background activity exceeded 4-5% of the maximum voluntary contraction, the onset latency of the M1 segment and duration of the M1 and the M2-3 segments remained constant (within ± 2 msec) for different magnitudes of step load displacements, despite marked variation in the range of the displacement's amplitude, duration, velocity, and acceleration. We propose that the dependency of the relationship between reflex magnitude and imposed movement parameters on tonic motoneuron activity, as represented by pre-existing EMG levels, may reflect an automatic adjustment mechanism that could be utilized in servo compensation of movements requiring markedly different force levels.

RÉSUMÉ: Nous avons comparé chez 30 sujets normaux l'activité EMG d'arrière-plan pré-existante et celle réflexe provoquée par un déplacement passif du poignet. Les plans de réponse "input-output" démontrent que l'amplitude des réflexes M1 et M2-3 est dépendante des paramètres de déplacement et du niveau d'activité EMG pré-existante. Se le niveau d'activité d'arrière-plan excède de 4 à 5% du maximum de la contraction volontaire, la latence de début de M1 et la durée de l'activité M1 et M2-3, par contre, semblent demeurer constant (± 2 msec) malgré la variation des poids des déplacements et malgré une grande variété d'amplitude, de durée, de vitesse, et d'accélération. Nous proposons que la dépendance à l'égard de l'activité tonique du motoneurone, de la relation entre l'ampleur du réflexe et les paramètres de mouvement représentée par les niveaux EMG pré-existants, ceci reflète l'ajustement automatique qui serait utilisé comme rétro-compensation pour les mouvements exigeant des niveaux de force différents.

Can. J. Neurol. Sci. 1984; 11:272-280

Over the last thirty years, electromyographic (EMG) activity evoked by imposed angular joint displacements has been used to study reflex systems responding to sensory input from limb mechanoreceptors. Both the analysis techniques employed and perspectives as to the peripheral and central neural mechanisms underlying the responses have evolved markedly since Hammond (1954) first described the segmentation of the biceps EMG activity evoked by imposed extension of the human elbow (see Wiesendanger and Miles, 1982 for a recent review).

Initially, most of the interest focused on the latencies of the different EMG segments (Hammond, 1954; Melvill Jones and Watt, 1971; Marsden et al., 1972; Tatton et al., 1975) as providing a possible means of elucidating the central connections involved in the generation of the responses. The latency considerations were based on the assumption that each of the EMG segments (now frequently labelled M1, M2 and M3) were mediated by

separate central pathways with different "loop times". More recently, the latency assumption has been questioned and a number of alternate central and/or peripheral mechanisms that may contribute to the generation of the segmented EMG responses have been proposed (see Eklund et al., 1982 and Lee and Tatton, 1982 for references and considerations of possible mechanisms).

Although research has not yet been able to unambiguously define the relative roles played by the various proposed mechanisms, it has been established that the involvement of specific CNS structures in the generation of the segmented responses can differ depending on the species and/or joint-muscle system examined. For example, the M2 segment of distal upper limb flexor muscles in primates is dependent on the integrity of the motor cortex for its elaboration (Lenz et al., 1983b), and spike triggered averaging has shown motor cortical

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Received November 10, 1983. Accepted for publication March 5, 1984

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neurons must contribute to the generation of the M2 segment in monkey wrist muscles (Cheney and Fetz, 1983). A similar dependency is not evident for the M2 segment evoked in the proximal limb flexors in the same animals (Miller and Brooks, 1981; Lenz et al., 1983a, 1983b) or for the second segment in the cat triceps (Ghez and Shinoda, 1978; Tatton et al., 1983). Hence, the evidence related to peripheral and central mechanisms and the resultant response properties determined for one joint-muscle system do not necessarily hold for another.

Other research has been directed toward determining the functional role of the segmented responses in the control of movements. Initially, research using imposed movements of the human thumb (Marsden et al., 1972) and ankle (Melvill Jones and Watt, 1971) was interpreted as suggesting that the responses were appropriate to "automatically" compensate for unexpected loads encountered during a voluntary movement. Subsequently, a number of other proposals for the functional role of the responses have been offered. For example, it has been proposed that the segmented responses may serve as "test pulses" to measure unexpected loads (Allum, 1976) or alternately, to maintain constant muscle stiffness despite changing loads (Kwan et al., 1979). As one step in exploring the validity of the different proposals, the input-output relations for the segmented responses have been examined. Averages of the rectified EMG responses have shown them to be monotonically graded with a number of related mechanical parameters for movements imposed on the cat elbow (Ghez and Shinoda, 1978; Tatton et al., 1983), the primate wrist (Tatton and Bawa, 1979; Jaeger et al., 1982a; Lenz et al., 1983b) and the human ankle (Gottlieb and Agarwal, 1979).

Several of the input-output studies attempted to control for variations in the excitability of the motoneuron pool innervating the stretched muscles (for an example see Marsden et al., 1976 as well as Tatton and Bawa, 1979 for details concerning the necessity of controlling for changing levels of motoneuron excitability). Yet, despite recognition of the likely importance of the level of pre-existing motoneuron excitability, its effect on the magnitude and timing of the segmented responses relative

to that of changes in the mechanical parameters of the imposed movements has not been systematically determined for any joint-muscle system. Accordingly, we have examined the time course and grading of the segmented responses in one joint-muscle system, the human wrist flexor muscles, to step load imposed angular displacements relative to changing background levels of motoneuron activity.

In response to step loads, the segmented EMG responses are shown to constitute constant duration pulses of activity whose input-output relations can be described by response planes relating their magnitude simultaneously to both the level of pre-existing EMG activity in the stretched muscle and the initial velocity of the imposed displacements. It is shown that determinations of the volumes containing the response planes for populations of normals should be used if alterations in the segmented responses induced by different movement paradigms or in patients with various neurological conditions are to be meaningfully assessed.

METHODS

The normal population in this study consisted of 30 subjects ranging in age from 10 to 65 years (the distribution is presented in the companion paper Tatton et al., 1984). All subjects were free of any musculoskeletal problems of the arm, or of any neurological disorders which might influence the results.

The subject's wrist was rapidly displaced by a D.C. brushless torque motor, under computer control (for details see Tatton and Lee, 1975). The manipulandum allowed the subject's wrist to sweep 50 degrees into either flexion or extension while maintaining its centre of rotation coaxial with the motor. The centre of this arc was predetermined to be the ray projecting from the centre of the elbow through the wrist and handle manipulandum. All imposed displacements were initiated within a narrow zone of ± 4 degrees from this defined centre. Five different step loads, in either the flexion or extension direction, were presented to the subject. The size of load, direction, duration, and the delay between displacements were randomly

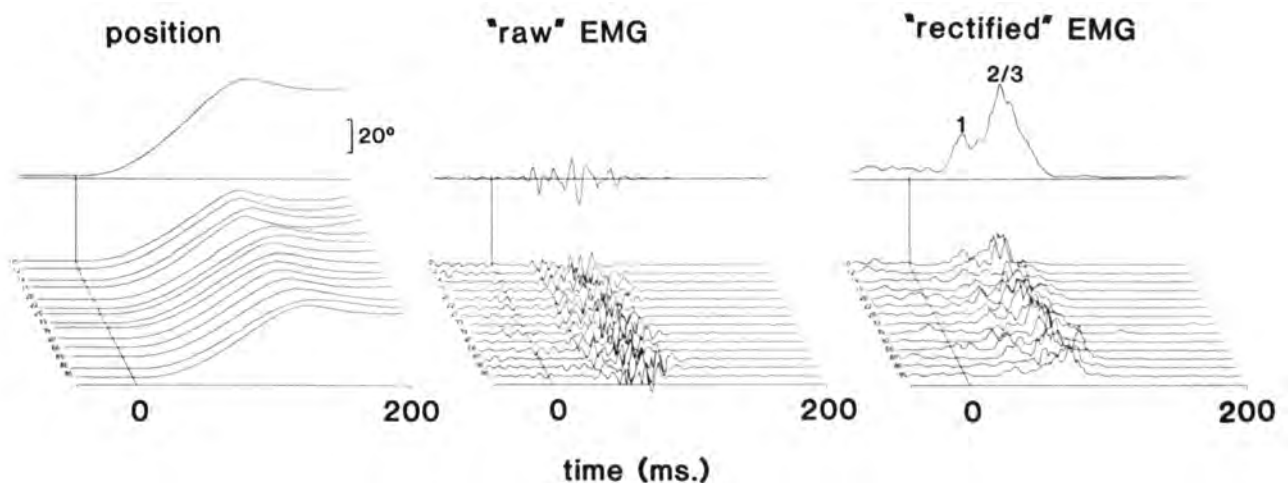


Figure 1 — Raster of the averaged handle displacement, "raw" EMG (i.e. filtered but unrectified), and corresponding rectified EMG activity measured for 14 step load perturbations of the same magnitude. The top trace represents the average activity and the serial traces plotted below are the individual trials that contribute to the average. See text for further details.

calculated by the computer to eliminate the possibility of any anticipatory reactions by the subject.

Pairs of surface EMG recording electrodes were placed over flexor carpi radialis (FCR) and extensor digitorum communis (EDC) near the junction of the proximal and middle third of each muscle. Differentially amplified EMG activity (half amplitude bandwidth 30-3kHz), wrist position and tension were simultaneously recorded with an 8-track FM tape recorder (bandwidth D.C. to 5kHz) throughout the experiment. A computer tape code was also recorded which signalled the onset of the step loads and encoded information concerning the magnitude, direction and temporal characteristics of each step load. A minicomputer subsequently digitized the analog signals at a 1 kHz sampling rate and stored the data on magnetic disc.

Averages of EMG activity and wrist position for 12 to 30 individual presentations were constructed for each size of step load. Figure 1 illustrates the averaging procedure for a single step load. A logic program automatically sorted the randomly presented trials according to step load magnitude. The program ensured that the individual displacements, sorted for a given step load magnitude and used to construct an average, were similar in their time course. Randomly occurring variations in the activity of muscles acting across the joint can result in changes in the stiffness of the joint-muscle system for one step load presentation as compared to another. Hence, the time course of the displacement resulting from a given step load magnitude can vary markedly. To make certain that each average angular displacement was representative of the individual displacements used in its construction, the computer program eliminated trials in which the position profile deviated from the normal average by more than 5% at specified grid crossing times. This procedure avoided the potential error that might occur due to averaging the EMG responses to a number of displacements with markedly different temporal characteristics. That is, even though the average displacements for two significantly different series of displacements might be identical, non-linearities in the input-output relations (see Tatton and Bawa, 1979) would be expected to result in average EMG responses with different magnitudes.

The fourteen sorted displacements presented in the lower portion of the panel labelled "position" in figure 1 were used to construct the average record in the panel's upper portion. The 44 msec period to left of the zero time (the step load onset) ensured that the wrist was maintained in a stationary position prior to the presentation of each step load. Traces which revealed the wrist to be moving at the time of the step load presentation were eliminated from the averages.

The panel labelled "raw EMG" presents the activity evoked by the fourteen displacements in the lower portion together with the average in the upper portion. The EMG was rectified prior to constructing the averages for analysis as shown in the panel labelled rectified EMG. This was necessary so that the relationship between the level of the pre-existing EMG activity to the left of time zero and the responses, denoted M1 and M2-3 (see Lee and Tatton, 1982), was maintained. Averaging unrectified EMG would cause the magnitude of the relatively "time-locked" M1 and M2-3 responses to increase over the pre-existing background EMG (which occurs randomly with regard to the step load onsets) by the square root of the number of events used to construct the average. In contrast, rectification allows the level of pre-existing EMG over the 44 msec prior to the step

load onset to be used as an estimate of the baseline motoneuron excitability which can be compared directly with the magnitude of the segmented responses.

The averaged records were then quantitatively analyzed by a statistical computer program. The mean level of pre-existing EMG activity was calculated together with its 3.0 standard deviation level (shown as MEAN and 3SD in figure 2). The latency and offset of the responses were measured from the intersections of the 3SD level with the average response traces as illustrated by the 28 and 92 msec vertical cursors in figure 2. The division between the M1 and M2-3 segments usually did not decrease to the 3SD level and was estimated from the point where the rising phase of the M2-3 peak was maintained for greater than 10 msec as illustrated by the 54 msec vertical cursor in figure 1.

The magnitude of the background EMG was measured in microvolts/msec and the magnitude of the response segments was similarly measured as the mean level of activity, above background, between the 3SD "cut-off" lines. The average level of pre-existing EMG and the averaged responses above that level were normalized against the mean voluntary activity of the stretched muscle during the phasic portions of 3-6 maximum isometric contractions (duration of each contraction 2-4 sec). The magnitudes of the background EMG and the segmented responses could then be expressed as a percentage of the maximum voluntary activity (% MVA).

The initial velocity of the wrist/handle manipulandum was measured as the change in position during the first 35 msec of displacement, taking into account the inherent electro-mechanical lag time determined for the system (10 msec). The onset of the force stepload marked the beginning of the imposed displacement

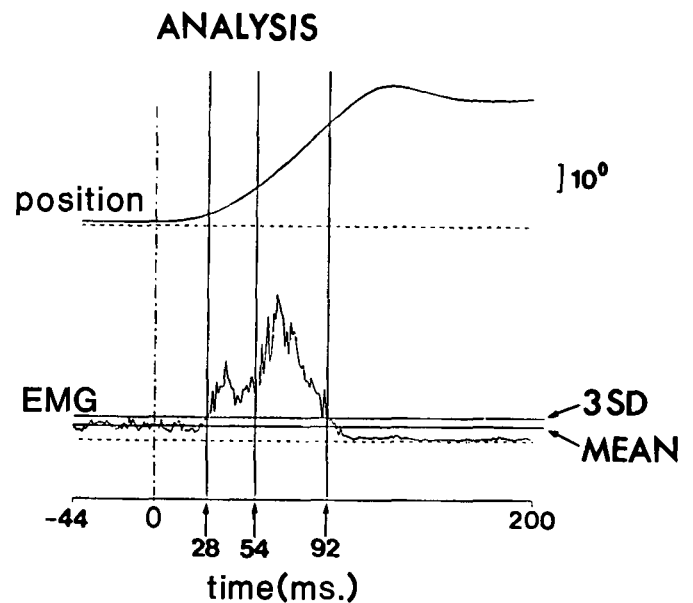


Figure 2 — Analysis procedures for the quantification of the magnitude, latency and duration of reflex activity. Mean background EMG activity is measured 44 msec prior to the onset of the step load and its three standard deviation (3SD) level calculated. The measured parameters were obtained from the intersection of the reflex EMG activity and the 3SD "cut-off" line. See text for details.

and starting time for temporal measurements of reflex EMG activity. Displacement prior to the earliest reflex burst was chosen as a reference to avoid contamination by refferent input, generated by the reflex response (see Tatton and Bawa, 1979 for rationale). In most of the analysis the velocity trace was computed by numeric differentiation of the position trace. For more precise analysis of the velocity and acceleration of the imposed movement, as shown by the A and D arrows in figure 3, a graphical simulation program that mathematically describes imposed motion in second-order systems was utilized (details and applications of this technique will be presented in a later manuscript).

RESULTS

The subjects were presented with a random series of step loads imposing extension or flexion displacements. Figure 3 presents a typical set of aligned traces for the average wrist position (upper traces), wrist velocity (middle traces) and their corresponding EMG activity (lower traces) for the stretched muscle (FCR) responding to each of the five different step load magnitudes imposing an extension displacement (preload of 0.2 Nm). Each of the corresponding sets of average records for position, velocity and rectified EMG for the largest to smallest

step load (1.4, 1.2, 1.0, 0.75 and 0.4 Nm.) is plotted serially from top to bottom. The numerals to the left of each average EMG record specify the mean background activity prior to the step load perturbation. The numerals to the right specify the mean level of reflex activity above background during the M1 and M2-3 segments, respectively.

It should be noted that when average background activity remains relatively constant (i.e., 7.4-9.3% MVA, in figure 3) the magnitude of both M1 and M2-3 activity is monotonically graded with the velocity of the displacement (Tatton and Bawa, 1979). The latency and termination of the responses as determined by the 3SD levels are marked by the L and T arrows respectively on each EMG record. The latencies and terminations, however, appear to remain relatively constant despite marked variation in the amplitude and duration of the imposed displacement (denoted by the P(max) arrows). Alternatively, with step load imposed displacements, the time of maximum acceleration (indicated by A arrows on the velocity records) varies by only ± 5 msec in contrast to the maximum deceleration which varies greatly (indicated by D arrows on the velocity records).

In figure 4, the magnitude of the M1 segment (above) and M2-3 segment (below) is plotted against the initial displacement

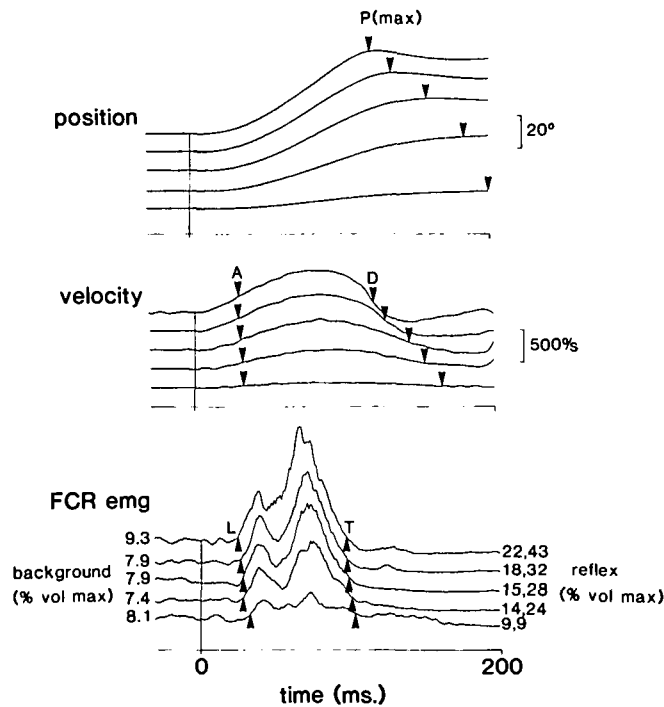


Figure 3 — Example of averaged results from a single individual to a series of five different magnitude step loads displacing the wrist into extension. The top and middle sections illustrate the five significantly different displacement and velocity profiles, respectively, generated by the different step loads. The maximum displacement for each step load is shown by an arrow under the P(max) symbol. The times of peak acceleration and deceleration are indicated similarly under the A and D symbols, respectively. The averaged activity from the stretched FCR muscle is shown in the bottom section. The background activity prior to the perturbation is shown to the left of each trace. The magnitude of the M1 and M2-3 activity is shown to the right of the traces (%MVA). The latency of the reflex activity is indicated by arrows under the L symbol while the termination is indicated by the arrows under the T symbol.

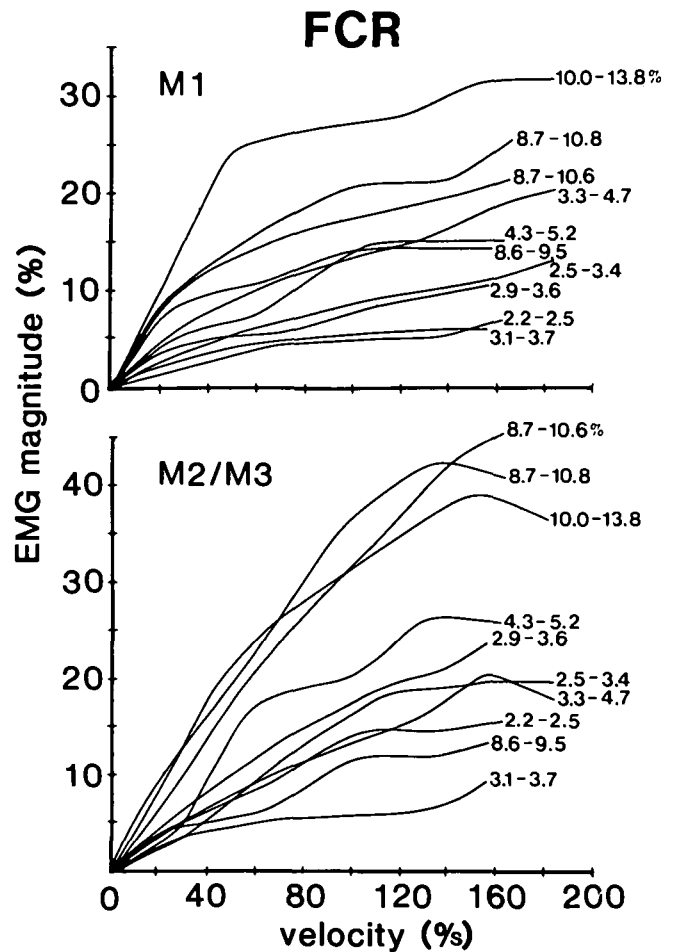


Figure 4 — Magnitude of the FCR M1 (upper section) and M2-3 (lower section) reflex activity with respect to increasing displacement velocity. Each line represents a single individual tested with five different step load magnitudes (N = 10). The numbers to the right of each trace represent the range of background EMG activity prior to the onset of the perturbation.

velocity for a population of normal subjects. For clarity, data from only 10 normal subjects, that are representative of the range in age and resting background EMG levels tested, have been presented. The amplitude of the M1 and M2-3 segments is on the ordinate while the mean velocity during the initial 35 msec of the imposed movement is on the abscissa. Initial velocity was utilized as the input variable in order to avoid "contamination" of the input parameter by refferent sensory activity due to the reflex movements produced by the responses (see Tatton and Bawa, 1979 for detailed discussion and rationale). To avoid confusion, the individual data points have been eliminated in this diagram but the discretely measured average values can still be inferred from the points of inflection along the continuous lines. All lines have been extrapolated to zero since the response EMG activity would be equivalent to the background EMG activity at this point. All subjects demonstrate a monotonic increase in magnitude of both M1 and M2-3 activity with increasing initial velocity as would be expected from the traces presented in figure 3. Examination of the plots reveals that individuals with higher resting background EMG levels tend to have greater response magnitudes for both the M1 and M2-3 segments for similar initial velocities.

As a means of investigating this interdependency, the magnitude of the responses was analyzed with respect to the two independent variables: 1) resting background activity; and 2) the initial displacement velocity. The mean values for the population were utilized to generate the three dimensional planes presented on the left side of figures 5 and 6 for the M1 and M2-3 segments, respectively. The logarithm of initial velocity was utilized as the X axis variable so that the response surfaces relating the three variables are planar and monotonic over the levels of background EMG (2.2 - 13.8% MVA) and velocities (up to 200 degrees/sec) examined. To construct the mean level response surface, logarithmic regression analysis (least squares error) of the responses from individual subjects provided the interpolative data for a grid matrix comparing background EMG, initial velocity, and reflex EMG. The "response planes" illustrate the dual dependence of the reflex magnitude on both the initial displacement velocity and the level of background activity immediately prior to the displacement onset. The points on the

response plane labelled A-D for the M1 segment in figure 5 facilitate consideration of the dual relationship. For example, points B and C have the same Y axis value (as represented by their height above the "floor" of the 3D diagram) but each differs markedly in background EMG levels (BKGD) and initial velocity (IV). Point C relates to a BKGD value of 10% MVA and an IV of 20 degrees/sec while point B relates to comparable values of 5% MVA and 60 degrees/sec. Each pair of BKGD and IV values would result in the same magnitude of M1 segment.

Points A and B when compared to C and D emphasize a second point. Even using a logarithmic scale for IV, the double slope of the plane is markedly sensitive to the BKGD level. Changes of as little as 2.0% MVA in background activity can double the reflex magnitude at high levels of initial velocity (i.e. 100-200 degrees/sec). A further illustration of how the slope of the surface changes along constant BKGD lines versus constant velocity lines is provided by comparing the slope of the dotted lines joining A to C and B to D to those joining A to B and C to D. The response planes make it evident that comparisons between different subjects are not meaningful unless both initial velocity (as a representative mechanical variable) and resting background activity values are presented. Finally, it is worthwhile to note that as BKGD increases, the threshold IV needed to evoke a reflex response correspondingly decreases.

The right hand portions of figures 5 and 6 present "response volumes" estimated to enclose the range of values for the normal subjects. Conceivably, these volumes could contain all the M1 or M2-3 segment values for any population of normal subjects, given measurement of both BKGD and IV. In this case, they must be viewed as preliminary due to the relatively small number of normal values used to calculate the volumes. If a number of subjects sufficient to determine whether the responses were normally distributed (i.e. several hundred) were used, then volumes could be calculated that would specify confidence limits (for example 99%) rather than ranges as presented in figures 5 and 6. Since ranges were used the M1 and M2-3 response volumes presented probably exceed the extent of a 95% or 99% confidence volume calculated using normal statistics.

To confirm the interdependence of the reflex magnitude on BKGD and IV, individual subjects had the resting background

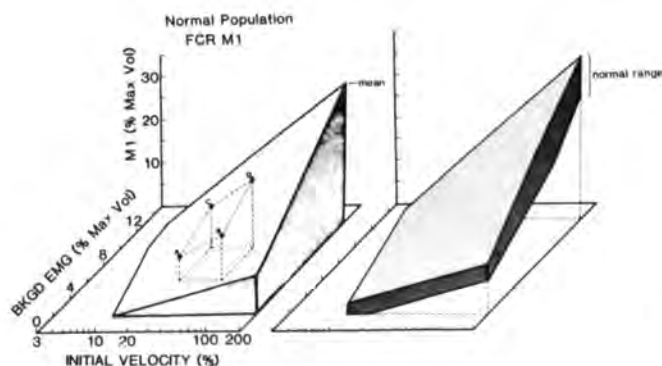


Figure 5 — Effect of pre-existing background EMG activity and initial displacement velocity on the magnitude of the M1 reflex response. The figure to the left illustrates the mean activity for the sample population shown in figure 4 (upper section). The figure to the right represents a volume containing the normal range of the subjects.

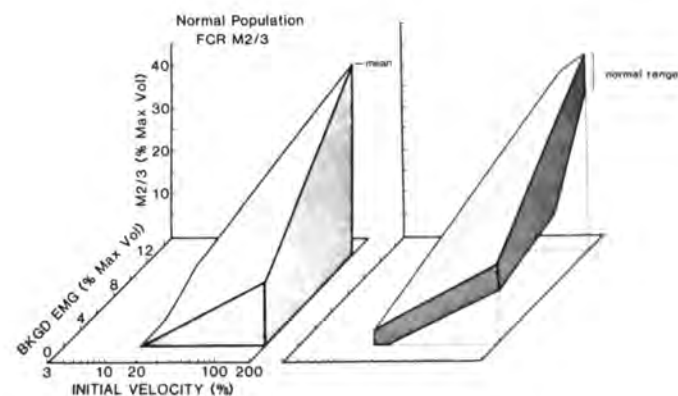


Figure 6 — Effect of pre-existing background EMG activity and initial displacement velocity on the magnitude of the M2-3 reflex response. The figure to the left illustrates the mean activity for the sample populations shown in figure 4 (lower section). The figure to the right represents a volume containing the normal range of the subjects.

EMG activity serially increased by maintained "preloads" (0.0 to 0.47 Nm.) while wrist displacements were randomly imposed. The insert plot in the upper left corner of figure 7 presents the relationship between increasing preload torque and background EMG activity. The main portion of figure 7 presents the family of semi-logarithmic input-output relations for the single subject's FCR M2-3 segment for each of the five preloads (curves obtained by logarithmic regression analysis, correlation coefficients within brackets; similar relations were measured for the M1 segment). It is evident that as the resting background activity increases, the slopes ("gain") of the semi-logarithmic relationships increase (from 6.4 - 9.2) while the minimum initial velocity threshold decreases (18 - 3.5 degrees/sec), similar to that predicted by the surface calculated for the normal population.

In order to determine if an individual subject with serially graded background EMG levels correlated to the population of normal subjects with inherently different resting background EMG levels the M2-3 response plane in figure 8 was calculated from the data illustrated in figure 7. This plane would be contained entirely within the M2-3 response volume in figure 6.

Despite the wide ranges of background activity, displacement velocities, displacement amplitudes and durations, the reflex EMG activity remains constant in latency and duration for step load imposed displacements. This is illustrated in figure 9 where the summed duration of the two segments (labelled M1/2/3 duration) is determined for the interval beginning at the initiation of the M1 segment (the L arrows in figure 3) and continuing to the conclusion of the M2-3 activity (T arrows in figure 3). Plots are shown for six representative normal subjects chosen for their different ranges of BKGD values. The upper plots illustrate

the inverse relationship between displacement duration and increasing step load magnitude. The lower and middle plots demonstrate the constant latency and duration of the reflex activity, respectively. In short, both latency and M1/2/3 duration

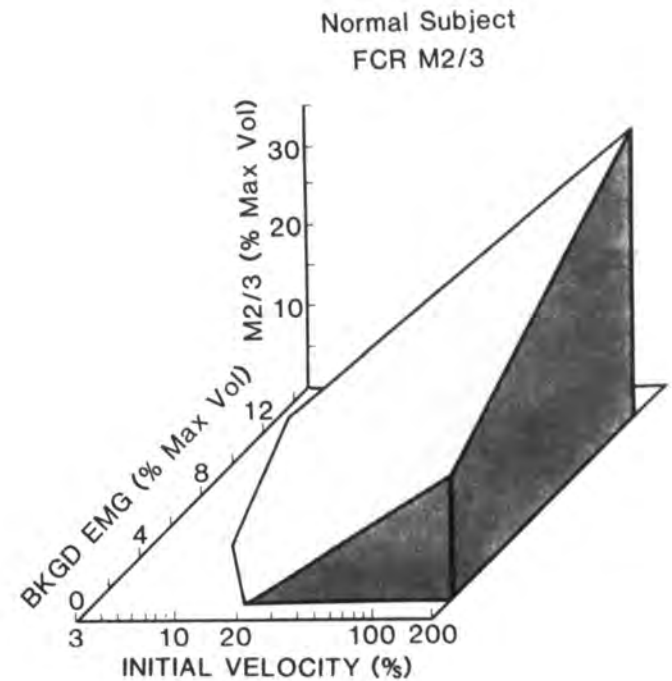


Figure 8 — Response plane created for a single individual from the data presented in figure 7.

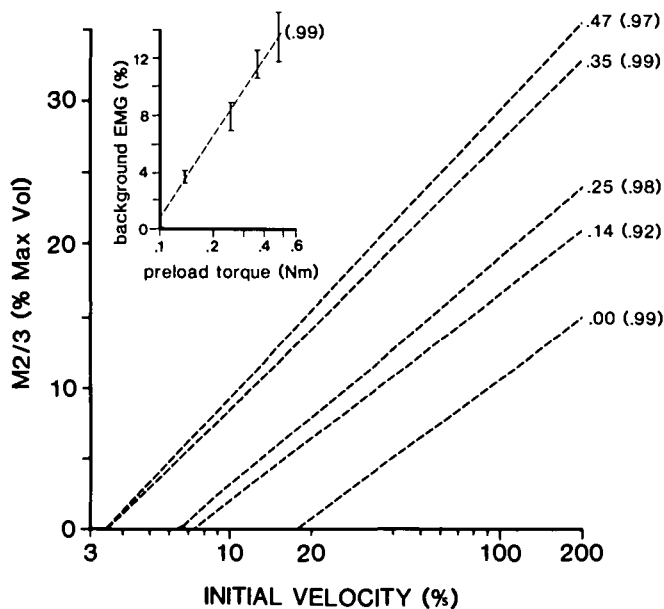


Figure 7 — Effect of initial velocity on the magnitude of the FCR M2-3 reflex response taken from a single individual. The background activity of the subject was serially increased by preloading the muscle with a tonic torque (see inset). Note that the 0 Nm preload was not used in the calculation of the logarithmic regression line. The numbers to the right of each trace represent the magnitude of the preload torque. The numbers within the brackets represent the correlation coefficient for each fitted curve.

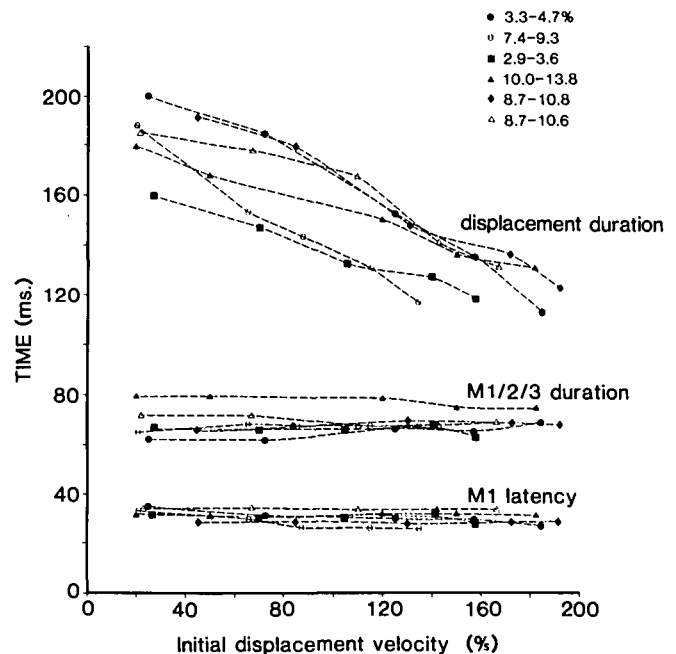


Figure 9 — Effect of initial displacement velocity on the displacement duration, M1/2/3 duration (total reflex duration), and the M1 latency for a representative sample of 6 subjects. Each subject is indicated by a separate symbol and the respective background activity is shown in the top right corner.

remain constant over a wide range of: 1) background activity (3.3-10.6% MVA); 2) initial displacement velocities (20-194 degrees/sec); and 3) displacement durations (120-200 msec). Specifically, for an individual subject the latency of the M1 and duration of the M1 and M2-3 segments is constant to within ± 2.0 msec.

Figure 10 presents the same variables for increasing levels of BKGD in an individual subject. The values remain constant with a relatively small variance (shown by the standard deviation bars) for BKGD levels exceeding 4-5% MVA. Below that level, onset latencies can increase significantly (i.e., by a mean value of 5 msec at BKGD = 2% MVA) and greatly increase in variance. Similarly, M1/2/3 duration decreases at BKGD levels below 4% MVA and shows greater variance.

DISCUSSION

Previous studies examining changes in the segmented responses (for example see Tatton and Lee, 1975) have not taken background levels of EMG activity in the stretched muscles adequately into account. Alternately, other studies recognizing the importance of this variable have attempted to maintain the background EMG at constant levels (for example see Tatton and Bawa, 1979) or when comparisons between responses were required, attempted to maintain background EMG at lower levels if the responses were expected to be increased (Lenz et al., 1983a). Both of these approaches are difficult given the marked sensitivity of the responses to small changes in background EMG in that even variations of 2-3% MVA in the background level could increase the response by 30-100% depending on the initial velocity.

The construction of the response planes requires that: 1) the 3SD level approach be used to avoid arbitrary determinations of the onset and offset times of the responses; 2) the activity be calibrated so that levels of EMG activity can be compared between subjects. We have chosen to measure the voluntary activity related to a maximal isometric contraction against which to normalize the background EMG and amplitude of the response segments. An alternate approach is to calibrate the activity

against the maximal response to direct electrical stimulation (see Lenz et al., 1983b and Verrier et al., 1984).

The validity of both approaches in the present human study relies on previous work describing the grading of the firing probability of single motor units (SMUs) in monkey wrist flexors to imposed displacements (Tatton and Bawa, 1979). Assuming homology between the two primate species (see Tatton et al., 1983), the observation that the response probability for SMU firing ranged only from 0.15 to 0.96 for a single displacement (despite maximal IVs and preloads) is relevant to the interpretation of the calibration methods. The SMU results indicate that increases in the amplitude of the response segments or in the level of background EMG are related to progressive recruitment of SMUs. Hence, the percentage maximum voluntary activity or the percentage maximum electrical response provides an estimate of the percentage of the motoneuron (MN) pool innervating the stretched muscle activated by the preload or the imposed displacement. Given significant factors such as the volume conductor properties of the forearm or the solid angle between the muscle fibres generating the myoelectric activity and the recording electrodes, the relation between the maximum voluntary activity and the percentage of the MN pool activated is likely to be a non-linear one. Yet, despite the probable non-linearity, this relationship provides a conceptual framework within which to consider the properties of the response planes.

For most subjects (see figure 3), the input-output plots at a given background EMG level maximized at IVs of less than 200 degrees/sec. This becomes even more evident on examining the response planes (figures 5, 6 and 8) at high levels of background EMG (i.e., 10-14% MVA). Subjects cannot maintain greater than 14% MVA for sufficient periods to properly study higher background levels. Hence, we do not have data on whether increasing background activity effectively saturates the reflex response similar to that of initial velocity, or whether in fact, the responses begin to decrease at higher background levels.

In any case, the planes could be interpreted as supporting the supposition that the compound postsynaptic potentials generated at the motoneuron pool by the sensory afferents activated by the displacements maximize for IVs of less than 200 degrees/sec. (or by other mechanical parameters related to the step loads). This interpretation is supported by the observation that there are continued increases in the responses if the background level of activity is increased, even at IVs of 200 degrees/sec. It could equally be argued that synaptic inputs generating the background activity also facilitated linking interneurons in polysynaptic pathways activated by the displacements. Facilitation of the linking interneurons could "amplify" the sensory input and thereby increase the responses. Finally, the proposal that increased excitability of the alpha MNs is a factor in background sensitivity gains support from the finding that the velocity thresholds for the responses decrease with increasing background EMG levels suggesting the MNs are closer to firing threshold.

Previous studies have reported that the magnitude of the various segments could be altered by prior instructions to "resist" as compared to prior instructions to "let go" (so called voluntary intent, Hammond, 1954; Tatton and Lee, 1975; Mortimer and Johnson, 1976) or with procedures that were intended to alter sensory input such as vibration (Hendrie and Lee, 1978) or ischemia (Jaeger et al., 1982b). Since these studies did not control for background EMG, the effect of the various procedures or instructions may have been either over or underestimated.

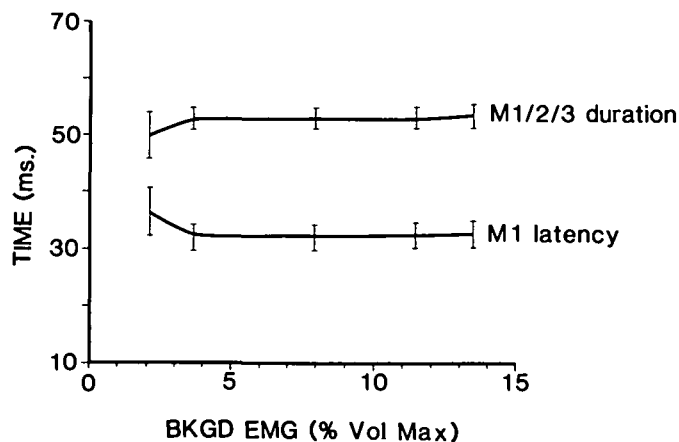


Figure 10 — Effect of increasing background EMG activity in a single subject on the latency of the M1 and the duration of the M1/2/3 reflex response. Bars indicate 1SD.

To adequately explore these phenomena, response planes should be constructed as in figure 8, both before and after the procedure or for the different instructions.

In the detailed presentation of their servo hypothesis for the long-latency responses, Marsden et al. (1976) recognized the effect of increasing load and the resulting increased levels of muscle activation on the "gain" of the responses (as illustrated by their expanded "tulips" in figure 14). They hypothesized that the gain control by the level of muscle activation served to automatically compensate for fatigue and maintain the performance of the servo. Over the last year, the proposal that the long-latency activity is generated, at least partially, by a transcortical reflex involving the motor cortex, especially for distal upper limb muscles, is gaining reacceptance due to recent lesion studies (Lenz et al., 1983b) and studies using spike-triggered averaging of motor cortical neuronal activity (Cheney and Fetz, 1984).

Hence, the original proposal by Phillips (1969) of a transcortical load compensating servo remains a possibility for distal upper limb muscles in primates. Accepting a servo function, despite the reports claiming inadequate feedback (see Marsden et al., 1981), the relatively high dependence of the responses on the level of background EMG revealed by the response planes could be taken to suggest a related but more fundamental function than one to compensate for fatigue. Rather the "gain" (EMG output/mechanical input) of the reflex would automatically increase depending on the force expended against a load (see the inset plot in figure 7 relating the maintained force necessary to oppose a preload and the level of background EMG). The force-background relationship would automatically adjust the level of servo compensation for movements requiring markedly different force levels i.e., compare a fine low load movement such as writing to a high load one such as carrying gold bars in a briefcase, both involving the wrist flexors. The surface of the planes would then describe at least part of the operational range for the automatic force adjustment.

The constant time course of the responses to step load imposed displacements could be taken to suggest that they function as constant duration, amplitude modulated pulses of EMG activity. This would be especially relevant when considered together with evidence provided by Bawa and Tatton (1979) that SMUs responding during the M1 segment were largely of the slow (S) twitch type and those responding during the M2-3 segment, largely fast (F) twitch type (see further evidence and discussion of this concept in Lenz et al., 1983a). Bawa and Tatton (1979) pointed out that, accepting division of twitch types according to response segment and taking the approximately 30 msec difference in time to maximum twitch between S and F motor units, the M1 and M2-3 engendered tensions would reach their maximum simultaneously. Hence, the responses in fact would constitute a single constant duration tension pulse.

Even though the response duration did not correlate with the duration of the displacement, its maximum velocity, initial velocity, or the time of maximum deceleration, the constant duration observation must be regarded with some caution due to the constancy (± 5 msec) of the time to maximum acceleration produced by the step loads. At present, the relative contribution and timing of muscle, cutaneous and joint afferent volleys to the segmented responses is not clearly defined (see Lee and Tatton, 1982 and Verrier et al., 1984 for relevant discussion). Hence, the physiological basis for the constant termination

time of the responses is conjectural. If, in fact, the acceleration profile determined the time course of the reflex activity then a series of imposed movements with a wider range of times to maximum acceleration would show a commensurate variation in response duration.

ACKNOWLEDGEMENT

The research was supported by MRC grant MT5218, a Dystonia Foundation grant and funds from the C. Saunderson Memorial Swimathon. W. Bedingham was supported by a Dystonia Foundation studentship.

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