

1043
N82-13708

LOAD COMPENSATING REACTIONS TO PERTURBATIONS

AT WRIST JOINT IN NORMAL MAN

R. J. Jaeger, G. C. Agarwal, and G. L. Gottlieb

Bioengineering Program
University of Illinois at Chicago Circle, Chicago, IL 60680
and
Rush Medical College, Chicago, IL 60612

SUMMARY

The electromyographic responses to step torque loads were studied in flexors and extensors at the human wrist. Based on temporal bursting patterns and functional behavior, the response was divided into four temporal components. Two early components, the myotatic (30-60 ms) and late myotatic (60-120 ms) appear to be reflex responses. The third postmyotatic component (120-200 ms) appears to be a triggered reaction, preceding the fourth, stabilizing component (200-400 ms). A comparison of responses at the wrist with similar data at the ankle provides the basis for a generalized classification of the responses in various muscles to torque step perturbations.

INTRODUCTION

The study of human motor control has recently seen a number of reports on the electromyographic (EMG) response of single muscles to highly contrived perturbations in carefully controlled laboratory situations. Since the work of Hammond (1956), many investigators have used the limb perturbation paradigm in an attempt to answer the question of how the human motor system responds to externally applied loads (Melvill Jones and Watt, 1971; Allum, 1975; Lee and Tatton, 1975; Marsden *et al.*, 1976; Evarts and Granit, 1976; Crago *et al.*, 1976; Gottlieb and Agarwal, 1976, 1979; Thomas *et al.*, 1977; Hagbarth, *et al.*, 1981; and others). As artificial as this paradigm is, it has remained the choice of many investigators. This is,

Presented at the Seventeenth Annual Conference on Manual Control, UCLA, June, 1981. This work was supported in part by National Science Foundation Grant ENG-7608754 and grants from the National Institutes of Health NS-00196 and NS-12877.

first, because of our lack of understanding and agreement at this most simple and controlled level, and second, because of the added complexities and technical problems involved in attempting to study the response of the motor system to perturbations in more complex paradigms.

One of the intriguing questions about the response of the human motor system to externally applied loads has been the extent to which it is achieved by reflex action versus voluntary action (see Weisendanger, 1978). Along with this question has been the as yet unresolved controversy concerning the neuroanatomical pathways mediating some of these responses. Views differ over the relative involvement of the cerebral cortex (e.g. Marsden et al, 1973). An alternative scheme links the responses to segmental mechanisms which mediate multiple bursts of afferent activity (Hagbarth et al, 1981). One purpose of the present study was to determine to what extent the EMG responses of wrist flexors and extensors to torque steps are mediated by reflex processes.

One might wish a hypothesis of the mechanisms for these responses to be applicable to the entire human motor system. Unfortunately, when the results from the more commonly studied muscles are compared, different muscles appear to have quite different responses to similar torque perturbations. This can give rise to different and even conflicting hypothesis of load compensation. For example, an early hypothesis suggested that the response of the human motor system to externally applied loads was to regulate length, and this hypothesis is commonly referred to as load compensation (Merton, 1953). A more recent hypothesis suggested that muscle stiffness was being regulated (Houk, 1980), that is, the system regulates both length and tension to maintain a certain level of stiffness.

Differing experimental observations and their explanatory hypothesis arise in part from the use of different muscles, or from slight differences in experimental paradigms among investigators. There are also the concomitant differences in terminology (e.g. FSR of Melvill Jones and Watt, 1971; M1-M2-M3 of Lee and Tatton; SL-ML-LL of O'Riain et al, 1979; myotatic-postmyotatic of Gottlieb and Agarwal, 1980a).

Another purpose of the present study was to describe a data base of the EMG responses in wrist flexors and extensors that would be directly comparable to an existing data base on the ankle flexors and extensors (Gottlieb and Agarwal, 1979, 1980a, b) using similar paradigms and subjects. This comparison is interesting in that it gives some indication of the possibility of devising a generalized classification of the response of the human motor system to externally applied loads, at least with regard to similar joints in the upper and lower extremity. Given the functional and anatomical differences between human upper and lower limbs, it is by no means obvious that a meaningful comparison would be possible, but such

proves to be the case. Such a general classification scheme is a useful step in formulating a unified understanding of the human motor responses to mechanical perturbations.

METHODS

All experiments were performed using 8 normal human subjects of both sexes, between the ages of 20 to 40 years. A subject sat comfortably in a chair next to the apparatus. The upper arm was abducted about 45 degrees, with the elbow flexed about 90 degrees. The forearm was aligned in the device, and either rested on a long foam pad or was supported by elbow and distal forearm supports. The wrist was positioned such that the axis through the head of the capitate about which flexion and extension movements occurred, coincided with the vertical axis of the shaft of a D.C. torque motor (Inertial Motors, Model 06-024) mounted below the wrist. An aluminum bar was directly coupled to the shaft of the motor, and an adjustable flat paddle was bolted to the bar. The subject's hand, with fingers extended, was strapped flat to the paddle by three straps. Heavily padded mechanical stops limited the flexion and extension to about 75 degrees on either side of the relaxed neutral position. An oscilloscope display was provided with a reference target dot (finely focussed) and a movable response dot (diffusely focussed, about 3 times the width of the target dot) the position of which was continuously proportional to joint angle. This display assisted the subject in always using the same neutral rest position throughout the experiments. This apparatus restricted wrist motion to flexion and extension. No abducting and adducting movements could occur. A schematic of the experimental apparatus is given in figure 1.

Torque was measured by four semiconductor strain gauges (BLH Electronics, SR-4) bonded to the motor shaft (Perry and Lissner, 1955). Angular position was measured by a rotating-plate, capacitive transducer (Trans-Tek, model 600). The motor was driven by a D.C. power amplifier (Inland Controls, Model 200B).

The EMG activity of the flexor carpi radialis (FCR) and extensor carpi radialis (ECR) was led off using redux creme column electrodes (Hewlett-Packard, model 14220A) with adhesive collars. The EMG signals were differentially amplified and band-pass filtered (100, 60-1000 Hz). This raw EMG signal was further amplified (15X), full-wave rectified, and finally passed through an averaging filter with a 7 ms averaging time (Gottlieb and Agarwal, 1970).

A digital computer generated the motor amplifier drive voltage. Typically, three levels of background torque or "bias" were used, with positive torques stretching the flexors. The computer digitized motor shaft angle and torque (at a rate of 250 samples per second) and FCR and ECR rectified and filtered EMGs (at a rate of 500 samples per second) for later analysis.

The basic experimental paradigm was to deliver one second long steps of torque, randomized in amplitude, direction and inter-step interval to flex or extend the wrist. This was repeated for three different torque bias levels (0.025, 0, and -0.025 kgm). The subject would be given one of four instructions on what to do when the torque step was received. These instructions were:

1. Do not react (DNR): Allow the motor to move the wrist without voluntary intervention.
2. React to target (RTT): React as quickly as possible to restore the wrist to its starting position.
3. React maximally (RMAX): React as quickly as possible to overcome it and move your wrist as forcefully as possible in the opposite direction, to the limits of the mechanical stops.
4. Assist (ASST): React by moving as rapidly as possible in the same direction to the limit of the mechanical stop.

Perturbation Experiments

Three series of perturbation experiments were performed. All three used random sequences of torque steps, evenly spaced between 0.07 and 0.25 kgm in magnitude, presented at random intervals of from three to six seconds. In the first series, sets of thirty torque steps were presented with five step amplitudes randomly presented six times each. Step direction (flexion or extension) was always the same during one set, and this was known to the subject. Twelve sets were taken for each subject, with different combinations of instruction (RTT or DNR), bias torque, and step direction. This first series is analogous to a simple visual tracking experiment in the sense that subjects received a uni-directional perturbation which required a simple uni-directional response.

The second series of experiments presented one hundred torque steps (ten amplitudes, randomly presented ten times each). In this series, the direction of the torque step was also random, with five of the steps flexing the wrist and five extending it, and this was known to the subject. Six sets of data were taken for each subject, using two different instructions (RTT or DNR) at three values of bias torque. This second experiment was thus analogous to a choice visual tracking test with regard to the two possible directions of the perturbing torque step to which the subject selected an appropriate response.

In the third series of experiments, sets of thirty torque steps of five amplitudes were randomly presented six times. Step direction was always the same and this was known to the subject. A constant bias torque (0.025 kgm, in the same direction as the torque step) was maintained in each set. A total of eight sets of data were collected for each subject, each with a different combination of instruction (RTT, DNR RMAX, or ASST) and direction of step/bias torque. Our subjects reported that the ASST instruction was the most difficult one to follow.

DATA ANALYSIS - PERTURBATION EXPERIMENTS

The data was analyzed, first, by averaging together the responses to torque steps of like amplitude and plotting the resulting ensemble averages versus time. The EMGs were then integrated over four selected response intervals: these were approximately 30-60, 60-120, 120-200 and 200-400 ms following torque step presentation. The first two intervals and the beginning of the third interval were chosen based on EMG bursting patterns found by inspection of the average plots. The boundary between intervals 3 and 4 and the end of interval 4 were chosen based on other considerations to be discussed later. The integrated EMG (IEMG) for each interval was corrected for the presence of background activity by subtraction of the mean IEMG level measured over a 50 ms interval before the torque step. There is some variation in these intervals between subjects which were determined by visual inspection of the data and adjusted in calculations of IEMG.

The IEMG for a given interval was then plotted versus the velocity of rotation, computed from the averaged angular velocity trace by digital differentiation 12-16 ms following the torque step, and a first-order, linear regression line was fitted. The slope of this line was taken as a measure of the gain of the reflex arc. For this reason, these plots are referred to as gain plots (see Gain of EMG Responses in discussion and Gottlieb and Agarwal, 1979, for further details).

The latencies of the first three EMG components were manually measured from individual records using an interactive graphics terminal. This was necessary because an unbiased measurement of latency cannot be obtained from averaged records.

REACTION TIME EXPERIMENTS

To compare the latencies of the perturbation-evoked EMG components against voluntary reaction latencies, another experimental paradigm was used to study visual and auditory voluntary reaction times, in a fourth series of experiments. Since no torque perturbations were used in these experiments the torque motor was used with velocity and position feedback circuits to provide a sensation of "springiness" rather than unimpeded rotation, which subjects reported as being helpful. For visual reaction times, the scope display was changed so that the computer controlled the position of the target dot which assumed one of three discrete positions on the screen: Center, and extreme right or left. The response dot moved along the same horizontal axis as the target dot.

The experimental paradigm allowed both simple and choice reaction times (SRT and CRT) to be measured. Initially, the target dot was at the center position. After a variable delay of three to five seconds it jumped left or right on the screen. The subject, instructed to track the target, chose the appropriate motion, a "choice" reaction. Once the target dot had moved and a response had been made, the target dot always returned to the center position,

again after a variable delay. Because the subject always knew the endpoint of the returning jump, this was a "simple" reaction.

Voluntary reaction times to auditory stimuli were studied in a similar paradigm. Here however, the target display was replaced with a voltage controlled oscillator, controlled by the computer to produce three distinct tones. The middle tone (≈ 330 Hz, "E") corresponded to the center neutral wrist position at rest. The low and high tones (≈ 150 and 500 Hz, "D" and "B", respectively) corresponded to the extreme joint positions of flexion and extension, respectively. To begin the experiment, the middle tone was presented for about 10 seconds. After a random delay, the middle tone changed to either the low or high tone with the subject instructed to perform the appropriate wrist movement as quickly as possible. This was the choice reaction. Following this, the middle tone was again presented and the subject made a simple response to the center. Positioning the wrist in the center position was aided by a moderate amount of position feedback to the torque motor.

DATA REDUCTION - REACTION TIME EXPERIMENTS

The data collection and reduction was identical for both visual and auditory reaction times. Following a stimulus presentation, one second of data were collected at 250 samples per second of joint angle and EMGs from FCR and ECR. Latencies were measured from individual EMG records and tabulated as simple or choice responses.

RESULTS

Nature of EMG Responses

Typical responses to step torque perturbations are illustrated in figure 2. These are ensemble averages of joint angle and EMG from the stretched muscle (either ECR or FCR) for a single amplitude of torque step, in both flexion and extension, at three levels of bias torque. In both ECR and FCR, the EMG responses to a torque step were partitioned into four bursts. These we shall refer to as the myotatic responses ($30-60$ ms), the late myotatic response ($60-120$ ms), the postmyotatic response ($120-200$ ms), and the stabilizing response ($200-400$ ms). The stabilizing response continued as long as the subject resisted the motor, but the first 200 ms were taken as representative. In some records, each of the first three bursts is separated by short periods of silence, while in others the bursts overlap. The postmyotatic and stabilizing responses almost always appeared to merge. The rationale for choosing the intervals $30-60$ and $60-120$ ms can be seen from the bursting patterns of figure 2. Similarly, the choice of about 120 ms for the onset of the third interval is clear. The choice of 200 and 400 ms as interval boundaries was somewhat arbitrary, but this will be treated further in the discussion. Within these intervals there was always variability in the latency of each burst but rarely enough to obliterate the peaks and valleys of the averaged data. In any case, this categorization of responses relies,

not upon our ability to visually distinguish bursting patterns, but to make other distinctions of a more functional nature.

For most subjects the myotatic response is the smallest. It is not always present, and with the DNR instruction or a bias torque of opposite sign to the step it is frequently suppressed entirely. The late myotatic responses were larger and were present in every individual record. The postmyotatic and stabilizing responses, present in the lengthening muscle only with the RTT or RMAX instructions, were larger still. They were absent with the DNR instruction. With the ASST instruction, the postmyotatic and stabilizing responses appeared in the shortening (assisting) rather than the lengthening muscle.

GAIN OF EMG RESPONSES

In the first and second series of experiments, all four intervals showed a linear and monotonic increase of IEMG with the velocity of stretch (except for the last two intervals with the DNR instruction when no responses occur). The linear regression lines converged on the origin. There are other mechanical variables which correlate well with the velocity of stretch, such as the deflection angle and the amplitude of the torque step. The IEMG would show a similar behavior if plotted against one of these. It is because of this correlation between velocity and torque that the stabilizing responses (200-400 ms) is proportional to the velocity measure we use. At the ankle joint, the response in the interval 200-400 ms is proportional to the torque level in the motor being opposed by the subject (Gottlieb and Agarwal, 1980a). While this was not explicitly investigated at the wrist, we expect the same to be true.

The gain of the myotatic response depended heavily on the bias torque as shown in figure 3. This was most evident with the DNR instruction but also true for instructions requiring a reaction (RTT or RMAX). The behavior of ECR and FCR were similar to each other. The gain of the late myotatic response behaved much like the gain of the myotatic response in its dependence on bias, as shown in figure 4.

In distinction from the two earlier responses, the postmyotatic and stabilizing responses showed little dependence on bias, as shown in figure 5. The behavior of ECR and FCR were similar to each other for the two later components as well. The gain plots of figures 3 through 5 are representative of data seen in all 8 subjects.

The average gain for each subject and each IEMG interval were computed for experiments of series one and two. No systematic effect of a known versus an unknown direction of the torque step was seen. A standard t-test was used to test the hypothesis that the mean gain for series one (known direction) was the same as the mean gain for series two (unknown direction). In 19 of 24 cases (4 intervals by 6 subjects) there was no significant difference. ($p < 0.01$).

The dependence of the EMG gain in the four intervals on the full set of

instructions (RTT, DNR, RMAX, and ASST) from experiment 3 is shown in the gain plots of figure 6. Here, four regression lines appear on each response interval plot corresponding to the set of instructions. All regression lines for a stretched muscle converge on the origin and show a linear, monotonic increase in IEMG with stretch velocity with the exception of the RMAX line for the 200-400 ms interval. Note that the lines for the ASST instruction in the 120-200 and 200-400 ms intervals are taken from the assisting rather than the stretched muscle.

LATENCY IN VISUAL AND AUDITORY STEP TRACKING

The results for voluntary step tracking (series 4) are summarized in table 1. A series of t-tests were run within subjects to test the hypothesis that mean SRT was the same as mean CRT. This hypothesis was rejected in all but 2 of 12 tests at $p < 0.01$, although in these two cases SRT was still less than CRT. The fastest reaction time was auditory SRT, followed by visual SRT, visual CRT, and auditory CRT. Although there was a greater disparity between CRT and SRT in the auditory paradigm compared to the visual paradigm, the differences were significant in both. The most important point in these reaction time data is that the well known dichotomy (Welford, 1976) exists between voluntary simple and choice responses to visual as well as to auditory stimuli within our experimental setup.

EMG LATENCY - TORQUE STEPS

Latency measurements of postmyotatic responses (120-200 ms interval) were on the order of 120-150 ms, with no clear cut dichotomy between simple and choice reaction times. This was verified by testing whether the mean SRT was the same as the mean CRT using a t-test, as shown in table 2. Latencies of the 30-60 and 60-120 ms components remained stable over all experiments. The latencies of the 200-400 ms components could not be accurately measured, due to the overlap encountered with the previous interval.

The coefficients of variation for the postmyotatic, visual, and auditory latencies are summarized for simple and choice situations in table 3. Note that variability of latencies in choice situations is larger than in the simple situation for visual and auditory reaction times, but not for postmyotatic latencies.

DISCUSSION

Uniqueness of Each EMG Component

Each of the EMG components observed in this study displayed its own characteristic set of properties. The earliest response, occurring in the 30-60 ms interval, is the myotatic reflex. Based on latency considerations, it is equivalent to the M1 response described by Lee and Tatton (1975). It is analogous to the tendon tap response and thus largely mediated by the primary spindle afferents (Matthews, 1972). The wrist myotatic response is

both weak and variable when compared to the late myotatic response in the same muscles, or to the myotatic response in the soleus (Gottlieb and Agarwal, 1979). The gain of the myotatic response depends heavily on both instruction and bias. In most subjects, it could be entirely suppressed under appropriate combinations of those variables. Its latency was stable in all paradigms.

The second response (late myotatic), occurred in the 60-120 ms interval. Based on latency considerations it is equivalent to the M2-M3 response of Lee and Tatton (1975). The afferent input mediating this response is uncertain, although it has been suggested on indirect evidence that the spindle may be the responsible receptor (Iles, 1977; Marsden et al, 1977; Chan et al, 1979). Recent data of Hagbarth et al (1981) suggests that multiple spindle discharges are responsible for the multiple reflex EMG responses observed in stretched muscles. However, the relationship between afferent stretch discharge and reflex EMG is not a simple one-to-one relationship. These authors noted that the EMG response often contained one less peak than the neural response. Other than the initial latency, the temporal correlation between peaks and valleys of the afferent activity and the EMG response is poor (see figs 6 and 7 of Hagbarth et al, 1981). The late myotatic response is much stronger than the myotatic response. Its gain could be modified by instruction or bias, but it was always present in every individual record. The latency of this response was stable over all data collected. There does not appear to be an equivalent late myotatic response in the soleus (Gottlieb and Agarwal, 1980a), although there may be an analogous response in the biceps and triceps (Thomas et al, 1977).

The postmyotatic response was present only for the instructions involving a voluntary reaction by the subject. It is not a reflex (Gottlieb and Agarwal, 1980a) and based on latency considerations, appears to be equivalent to what was described as voluntary activity by Lee and Tatton (1975).

Unlike its two predecessors, the postmyotatic response is not locked to the stretched muscle. Unlike visual or auditory reactions, the postmyotatic response shows no dichotomy between the simple and choice response situations. The gain curves of the postmyotatic response are like those of the myotatic and late myotatic responses for the RTT and RMAX instructions. They differ from the gain curves of the earlier responses in that they are insensitive to bias, and are zero when a DNR instruction is given. The postmyotatic response at the wrist appears to be quite similar to the postmyotatic activity occurring in the interval 100-200 ms in the soleus (Gottlieb and Agarwal, 1980a). It remains to be seen whether analogous postmyotatic activity exists in the biceps or triceps.

Finally, the stabilizing EMG response in the interval 200-400 ms occurs only for instructions requiring a sustained reaction. The IEMG for this component shows a monotonic increase with rate of stretch, except for the RMAX instruction, where a large offset is observed. The latency of this response could not be accurately determined.

Thus it appears that the EMG responses of wrist flexor and extensors may be partitioned into a minimum of four distinguishable intervals. Such a partitioning is compatible with the observed repetitive spindle bursting

described by Hagbarth et al (1981) but by itself such bursting cannot account for the observed functional differences between the different intervals.

One factor contributing to these differences may be the efferent fractionation of motor units in a similar experimental paradigm with monkeys (Bawa and Tatton, 1979; Tatton and Bawa, 1979). The differences may also reflect progressive recruitment and derecruitment of mechanisms from different levels of the motor control hierarchy. From the present study no definite conclusion can be drawn.

REFLEX VERSUS VOLUNTARY RESPONSES

In considering various temporal segments of the EMG response, the question arises as to where to place the dividing line between reflex and voluntary responses. A short and stable latency, usually associated with reflex responses, would reflect primarily neural conduction time with minimal CNS processing delays. Certainly the myotatic response satisfies this criterion and may be considered a reflex response. Inability to voluntarily suppress a response is also a characteristic generally attributed to a reflex. This should not be confused with the ability to "voluntarily" modulate a reflex response (e.g. the Jendrassik maneuver), as illustrated by the dependence of the myotatic response on bias of the present study.

Similar observations apply to the late myotatic response. Although its latency is longer this response has all the characteristics of a reflex. The reflex arc associated with this response has been the subject of much controversy (e.g. Desmedt, 1979). No major distinctions other than latency can be drawn between these two components from the data presented here.

The postmyotatic response presents more of a problem. Its latency is longer than the preceding myotatic and late myotatic responses, on the order of commonly accepted values of kinaesthetic reaction times (approximately 120 ms, see Chernikoff and Taylor, 1952). Of course latency alone is not a sufficient classification criterion for any response. The postmyotatic response is present only with an instruction requiring a voluntary reaction by the subject. It does not depend on bias torque as do the previous responses, nor is it restricted to the stretched muscle. These are "voluntary" characteristics.

The postmyotatic response has other characteristics which differ from other responses we would commonly accept as voluntary. First, with the instruction RTT, an increasing IEMG with velocity of stretch is expected and observed. With the RMAX instruction a large, constant and velocity independent IEMG would be expected. In reality, the gain plots for the postmyotatic response with these two instructions are indistinguishable. The gain characteristics of the postmyotatic and stabilizing responses for the ASST instruction (measured in the assisting muscle) were not as consistent as their counterparts in the stretched muscle for the RTT and RMAX instructions.

A second feature of postmyotatic responses is that they show no dichotomy

between simple and choice reaction situations as do voluntary reactions to visual and auditory stimuli. It has been reported that at least for one type of kinaesthetic reaction time, no dichotomy between two and higher choice response tasks was found (Leonard, 1959).

In view of the above dilemma, we consider the postmyotatic response to be poorly described by either of the terms "reflex" or "voluntary". We call this a triggered response (Crago et al, 1976, Gottlieb and Agarwal, 1980a).

The exact point at which the truly voluntary response commences is open to question. Estimates from visual and auditory reaction times suggest a value on the order of 180-220 ms. In the present study, 200 ms was chosen. An exact determination is perhaps beyond the realm of neurophysiological definition.

Symmetry of Responses

Inspection of figure 2 shows that flexor and extensor responses to stretch are similar, possessing a high degree of symmetry. It was impossible to distinguish between FCR and ECR responses given the criteria of the present study. The symmetry in responses at the wrist is sharply contrasted by the asymmetry observed in ankle flexors and extensors (Gottlieb and Agarwal, 1979, 1980a). The response of the tibialis anterior is more like the responses of the FCR and ECR. The soleus differs, having a much stronger myotatic response and lacking the late myotatic response.

Known versus Unknown Perturbation Direction

No consistent effect of prior knowledge of torque step direction on the gain for any interval was seen. This is not in agreement with previous data on the effects of expectation on EMG responses to torque steps at the wrist (O'Riain et al, 1979)

General Characteristics of Responses to Torque Steps

Comparing the EMG responses and reaction time data for the wrist flexors and extensors of the present study with comparable data for ankle flexors and extensors leads to a scheme for classification of these responses. The schematic EMG responses to torque perturbations, shown in figure 7, form the basis for the following discussion. A schematic voluntary response to visual or auditory stimuli is also shown.

A period of silence immediately follows the torque step. This reflects neural conduction delays. The myotatic response (M1) is the earliest response, occurring at a latency comparable to that of the tendon tap response. At the wrist, it is enhanced by instructions requiring a reaction, while at the ankle, where the response is more pronounced in the soleus, it is less dependent on the instruction. Nevertheless, the myotatic response always: 1) shows a linear, monotonic IEMG increase with stretch velocity, 2) appears only

in the stretched muscle, 3) has a stable latency for all instructions, and 4) is strongly dependent on initial bias conditions.

The late myotatic response is not present in all muscles. At the wrist and tibialis anterior at the ankle, it is stronger than the preceding myotatic response. Like the myotatic response, it always: 1) shows a linear, monotonic IEMG increase with stretch velocity, 2) appears only in the stretched muscle, 3) has a stable latency for all instructions, and 4) shows a dependence on the initial bias conditions.

Whether this general scheme of classification will be applicable to other muscles remains to be seen. Its most notable feature is the de-emphasis of latency as the primary classification criterion. It appears to be useful for comparing the EMG responses to torque perturbation in the flexors and extensors of both the wrist and ankle. It proposes a progressive change in dominance, from an early dependence of the response almost entirely upon the stimulus to an eventual volitional dependence which is only dependent on the stimulus when the subject chooses. The transition appears to take place in the 100 to 200 ms interval in which we observe the postmyotatic response. This transition interval appears to be the same at both the ankle and the wrist, indicating that conduction times between higher motor centers and the muscle play a small role in its determination.

REFERENCES

- Allum, J.H.J. Responses to load disturbances in human shoulder muscles: the hypothesis that one component is a step test information signal. Experimental Brain Research 22:307-326, 1975.
- Bawa, P. and Tatton, W.G. Motor unit responses in muscles stretched by imposed displacements of the monkey wrist. Experimental Brain Research 37:417-437, 1979.
- Chan, C.W.Y., Jones, G.M. and Catchlove, R.F.H. The electromyographic response to limb displacement in man II: sensory origin. Electroencephalography and Clinical Neurophysiology 46: 182-188, 1979.
- Chernikoff, R. and Taylor, F.V. Reaction time to kinesthetic stimulation resulting from sudden arm displacement. Journal of Experimental Psychology 43: 1-8, 1952.
- Crago, P.E., Houk, J.C., and Hasan, Z. Regulatory actions of the human stretch reflex. Journal of Neurophysiology 39: 925-935, 1976.

- Desmedt, J.E. (Editor) Cerebral Motor Control in Man: Long Loop Mechanisms. Karger, Basel, 1978
- Dufresne, J.R., Soechting, J.F. and Terzuolo, C.A. Electromyographic response to pseudorandom torque disturbances of human forearm position. Neuroscience 3:1212-1226, 1978.
- Evarts, E.V. and Granit, R. relations of reflexes and intended movements. Progress in Brain Research 44:1-11, 1976.
- Gottlieb, G.L. and Agarwal, G.C. Filtering of electromyographic signals American Journal of Physical Medicine 49:142-146, 1970.
- Gottlieb, G.L. and Agarwal, G.C. Dynamic relationship between isometric muscle tension and the electromyogram in man. Journal of Applied Physiology 30:345-351, 1971.
- Gottlieb, G.L. and Agarwal, G.C. Stretch and Hoffman reflexes during phasic voluntary contractions of the human soleus muscle. Electroencephalography and Clinical Neurophysiology 44:553-561, 1978.
- Gottlieb, G.L. and Agarwal, G.C. Response to sudden torques about the ankle in man: myotatic reflex. Journal of Neurophysiology 42:91-106, 1979.
- Gottlieb, G.L. and Agarwal, G.C. Response to sudden torques about the ankle in man: II - postmyotatic reactions. Journal of Neurophysiology 43:86-101, 1980a.
- Gottlieb, G.L. and Agarwal, G.C. Response to sudden torques about the ankle in man III: suppression of stretch evoked responses during phasic contraction. Journal of Neurophysiology 44:233-246, 1980b.
- Hagbarth, K.E., Hagglund, J.V., Wallin, E.U., and Young, R.R. Grouped spindle and electromyographic responses to abrupt wrist extension movements in man. Journal of Physiology (London) 312:81-96, 1981.
- Hammond, P.H. The influence of prior instruction to the subject of an apparently involuntary neuromuscular movement. Journal of Physiology (London) 132:17p-180, 1956.
- Houk, J.C. Regulation of stiffness by skeletomotor reflexes. Annual Review of Physiology 41:99-114, 1979.
- Hufschmidt, H.J. and Hufschmidt, T. Agonist inhibition as the earliest sign of a sensory-motor reaction. Nature 154:607, 1954.
- Iles, J.F. Responses in human pretibial muscles to sudden stretch and to nerve stimulation. Experimental Brain Research 30:451-470, 1977.
- Jaeger, R.J., Gottlieb, G.L., and Agarwal, G.L. Afferent regulation of stretch-evoked myoelectric responses. (manuscript in preparation)

- Lee, R.G. and Tatton, W.G. Motor responses to sudden limb displacements in primates with specific CNS lesions and in human patients with motor systems disorders. Canadian Journal of Neurological Sciences 2:285-293, 1975.
- Leonard, J.A. Tactual choice reactions. Quarterly Journal of Experimental Psychology 11:76-83, 1959.
- Marsden, C.D., Merton, P.A., and Morton, H.B. Is the human stretch reflex cortical rather than spinal? Lancet i:759-761, 1973.
- Marsden, C.D., Merton, P.A., and Morton, H.B. Stretch reflex and servo action in a variety of human muscles. Journal of Physiology (London) 259:531-560, 1976.
- Marsden, C.D., Merton, P.A. and Morton, H.B. The sensory mechanism of servo action in human muscle. Journal of Physiology (London) 265:521-535, 1977.
- Matthews, P.C.B. Mammalian Muscle Receptors and Their Central Actions. 1972.
- Melville Jones, G. and Watt, D.G.D. Observations on the control of stepping and hopping in man. Journal of Physiology (London) 219:709-727, 1971.
- Merton, P.A. Speculations on the servo control of movement. in Wolstenholm, G.E.W. (Editor), Ciba Foundation Symposium: The Spinal Cord, Little Brown, Boston, pp 247-260, 1953.
- O'Riain, M.D., Blair, R.D.G. and Murphy, J.T. Modifiability of the stretch reflex by prior information. Electromyography and Clinical Neurophysiology 19:57-63, 1979.
- Perry, C.C. and Lissner, H.R. The Strain Gage Primer, McGraw Hill, New York, 1955.
- Tatton, W.G. and Bawa P. Input-output properties of motor unit responses in muscles stretched by imposed displacements of the monkey wrist. Experimental Brain Research 37:439-457, 1979.
- Thomas, J.S., Brown, J., and Lucier, G.E. Influences of task set on muscular responses to arm perturbations in normal subjects and parkinson patients. Experimental Neurology 55:618-628, 1977.
- Welford, A.T. Skilled performance: perceptual and motor skills, Scott Foresman, Glenview, IL, 1976
- Wiesendanger, M. Comments on the problems of transcortical reflexes. Journal of Physiology (Paris) 74:325-330, 1978.

TABLE 1

COMPARISON OF SIMPLE AND CHOICE REACTION TIMES
FOR VISUAL AND AUDITORY STIMULI

VISUAL TRACKING

SUBJ	SRT			CRT			T	P
	MEAN	SD	N	MEAN	SD	N		
RJW	211	33	50	253	56	45	4.46	0.00
BKV	212	30	48	233	41	46	2.79	0.01
BMW	181	31	50	201	44	44	2.53	0.01
DVW	194	48	46	216	60	40	1.91	0.06
DMV	167	20	48	186	22	48	4.79	0.00
JGV	190	38	49	194	50	43	0.44	0.66

AUDITORY TRACKING

SUBJ	SRT			CRT			T	P
	MEAN	SD	N	MEAN	SD	N		
RJW	185	37	48	284	71	30	3.38	0.00
BKW	194	39	49	288	73	33	7.59	0.00
BMW	172	30	48	202	56	35	3.21	0.00
DVW	168	40	58	245	77	31	5.93	0.00
DMV	176	23	48	270	63	43	0.65	0.00
JGV	177	23	47	247	70	37	6.46	0.00

ORIGINAL PAGE IS
OF POOR QUALITY

TABLE 2

LATENCY OF POSTMYOTATIC EMG COMPONENT
IN SIMPLE AND CHOICE REACTIONS
TO TORQUE PERTURBATIONS

SUBJ	SRT			CRT			T	D
	MEAN	SD	N	MEAN	SD	N		
RJ1	131	17	126	123	15	217	-1.69	3.09
DV1	148	24	154	154	25	256	2.35	4.92
D11	113	13	148	114	13	246	3.74	4.46
JGV	142	23	129	133	23	193	-1.42	3.15
BJW	122	15	141	125	16	189	1.73	3.93
REV	156	24	148	156	19	223	0.94	1.40

TABLE 3

COMPARISON OF COEFFICIENTS OF VARIATION
FOR POSTMYOTATIC LATENCIES AND VISUAL AND AUDITORY REACTION TIMES

SUBJECT	SR	MIR	PBR		AUDITORY		VISUAL	
			S	C	S	C	S	C
RJ1	0.167	0.123	0.131	0.117	0.200	0.250	0.156	0.221
B11	0.164	0.132	0.149	0.121	0.174	0.277	0.171	0.210
DV1	0.212	0.122	0.162	0.162	0.233	0.314	0.247	0.273
D11	0.169	0.123	0.115	0.114	0.131	0.233	0.121	0.113
JGV	0.184	0.137	0.197	0.167	0.130	0.233	0.200	0.253

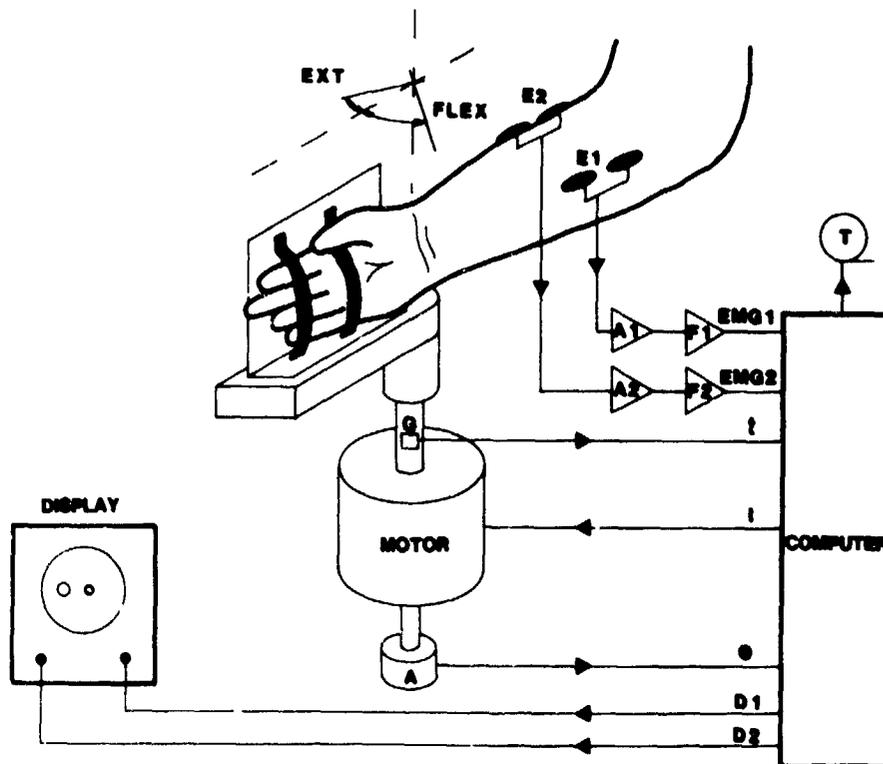


Figure 1: Schematic diagram of experimental apparatus consisting of a torque motor, whose current (I) was under the control of a computer. Joint angle (θ) is measured by a capacitive angle transducer (A), and torque (t) transmitted in the motor shaft is measured by strain gauges (G) bonded to the motor shaft. Electrodes ($E1$ and $E2$) led off the EMG through amplifiers (K) and filters (F). A visual display on the oscilloscope shows a reference target ($D1$) and joint position ($D2$). Data is stored off-line on digital tape (T).

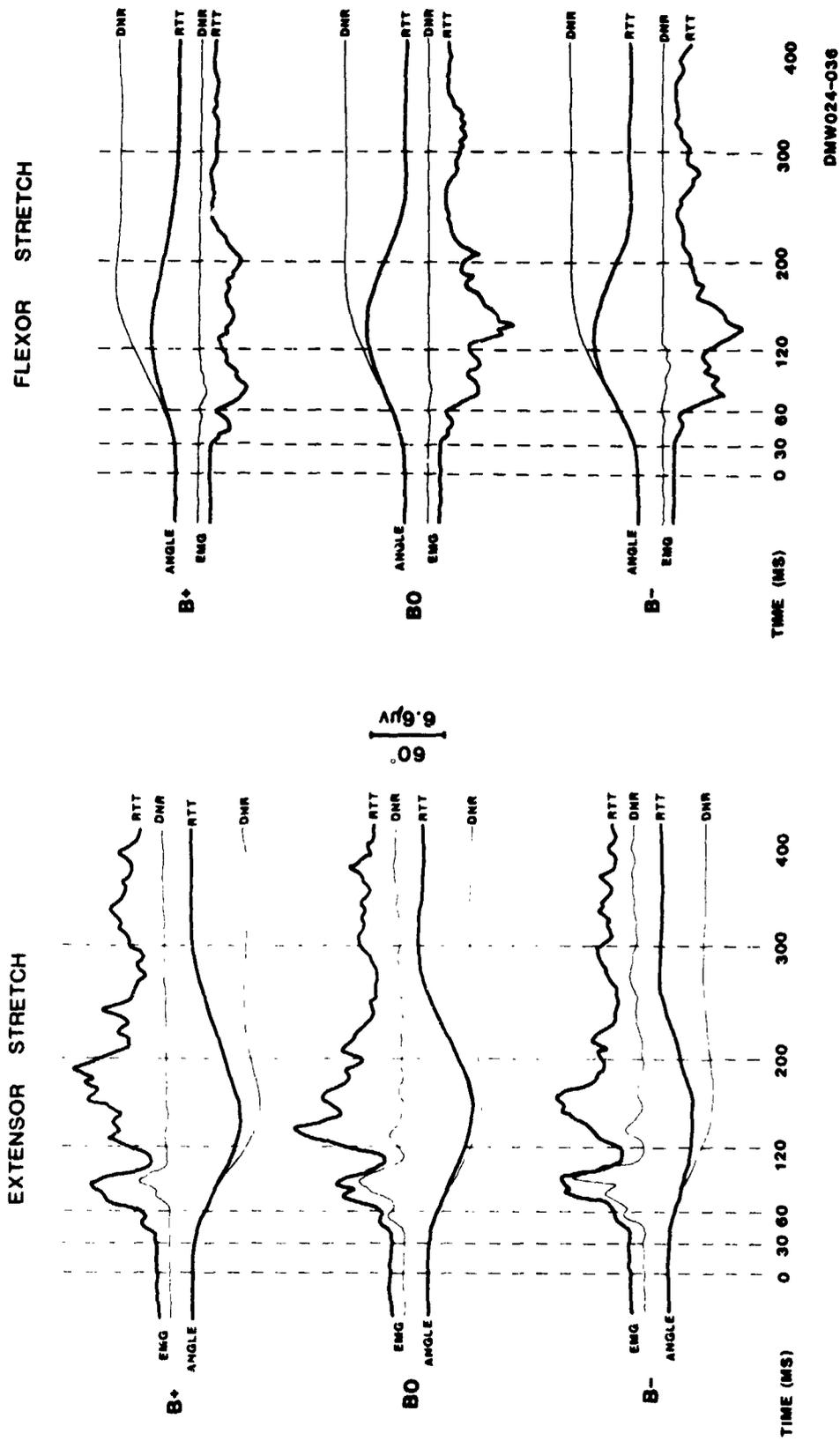


Figure 2: Joint angle and EMG responses to torque step in wrist extensor (A) and flexor (B) for three levels of bias. Instructions RTT (dark) and DNR (light) are superimposed. Torque steps are applied at time zero.

DMW024-036

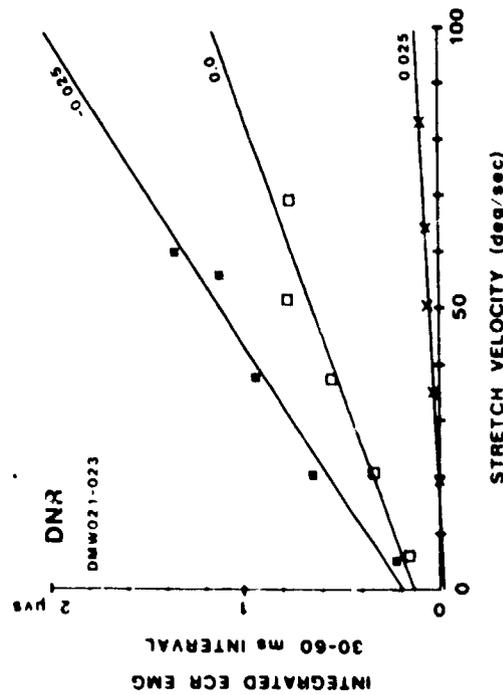
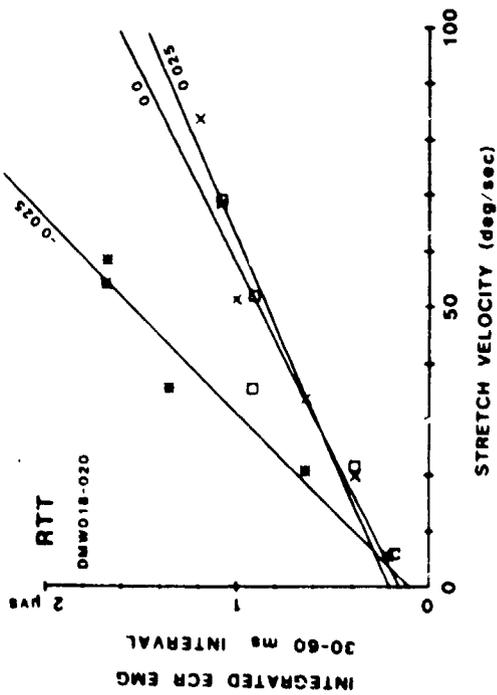
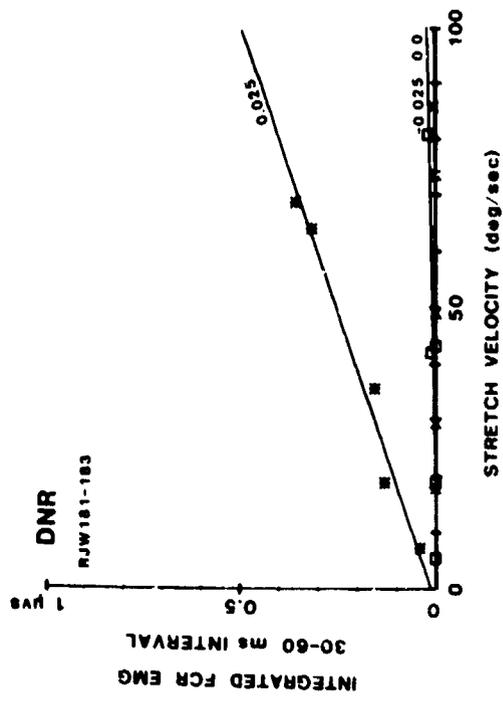
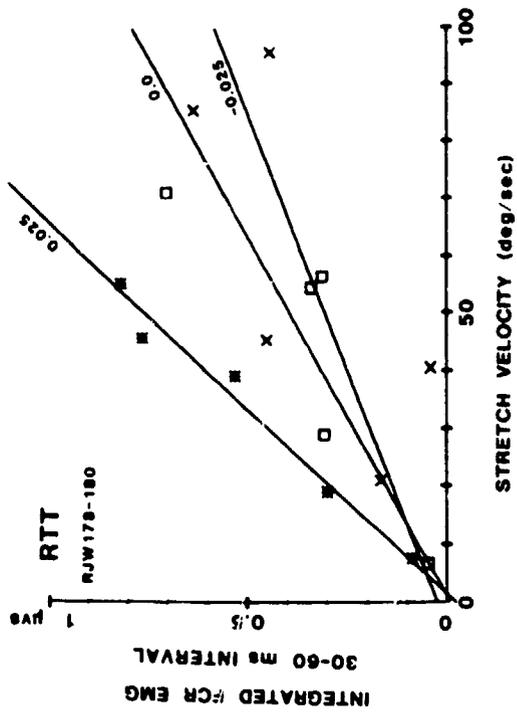


Figure 3: Gain plots for two subjects for myotatic response interval (30-60 ms). Top plots for the RTT instruction, bottom plots for DNR instruction. Data from ECR for subject DMW and FCR for subject RJJ. Plot symbols: *-facilitatory bias (bias and step have same sign), 0-zero bias, x-inhibitory bias (bias and step have opposite sign). Regression lines labeled with values of bias in kgm.

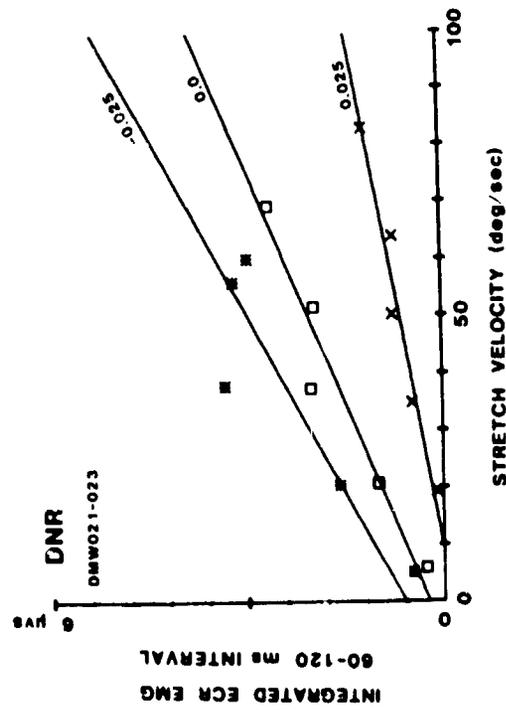
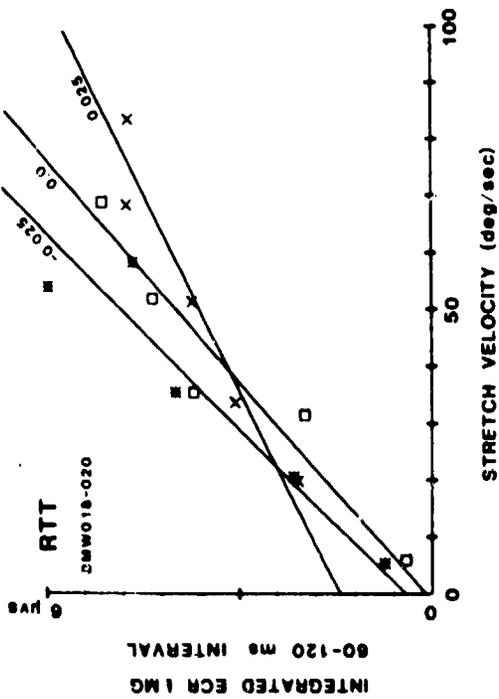
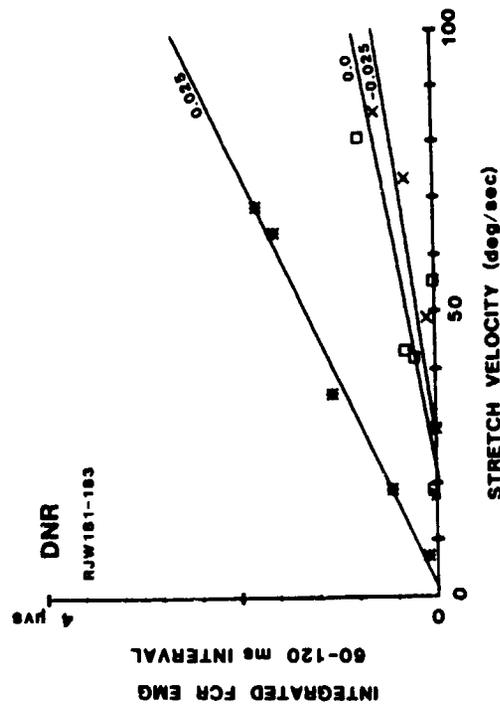
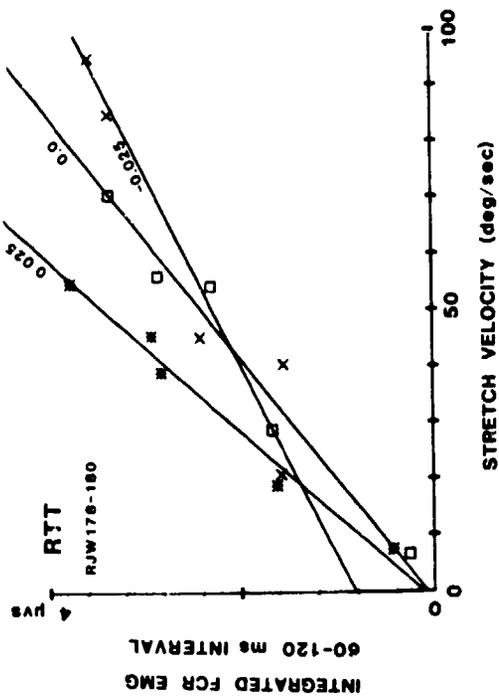


Figure 4: Gain plots for two subjects for late myotatic response (60-120 ms). Top plots for RTT instruction, bottom plots for DNR instruction. Data from ECR for subject DMW and FCR for subject RJW. Plot symbols: *-facilitatory bias (bias and step have same sign), o-zero bias, x-inhibitory bias (bias and step have opposite sign). Regression lines labeled with values of bias in kgm.

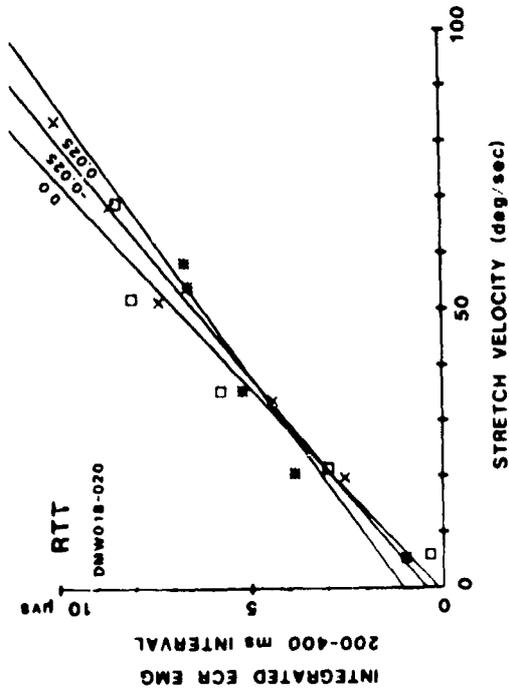
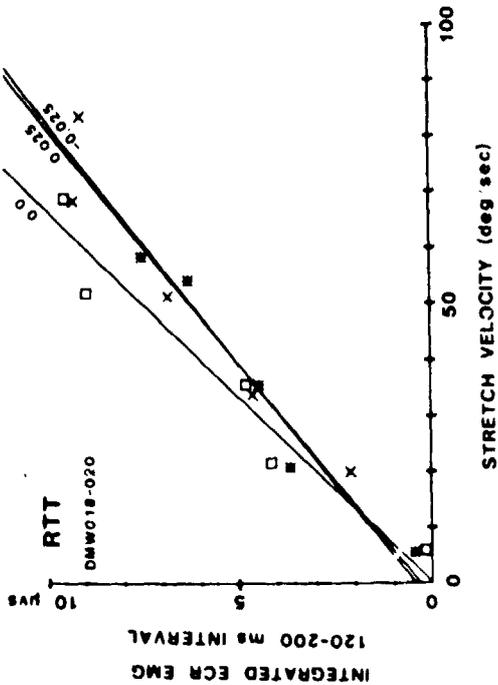
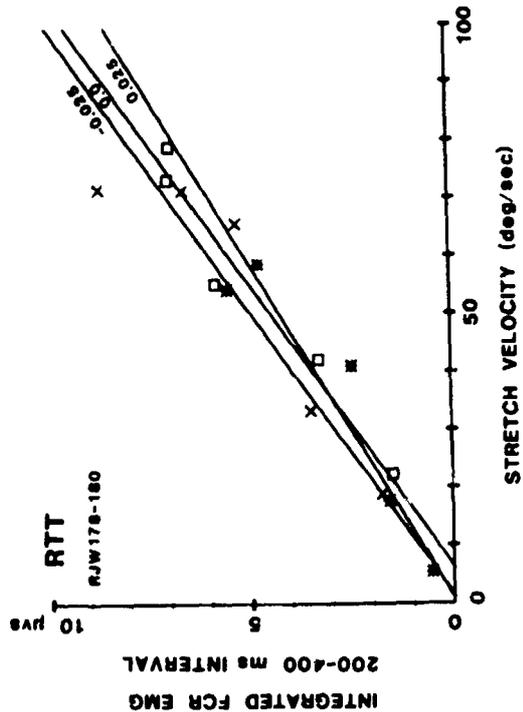
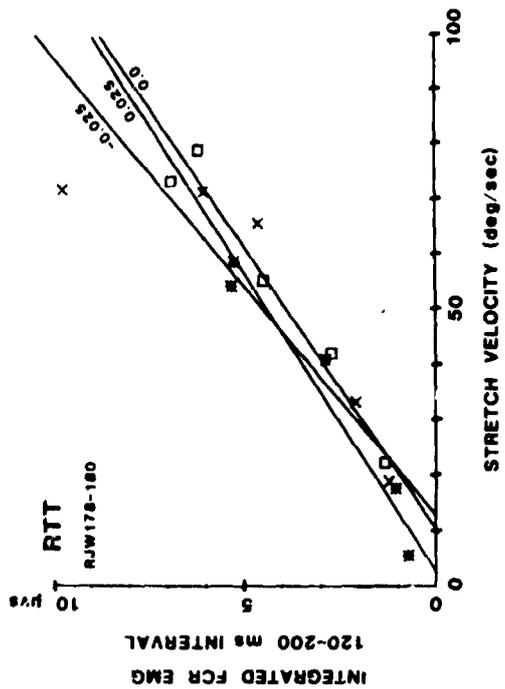


Figure 5: Gain plots for postmyotatic and stabilizing responses (120-200 and 200-400 ms intervals respectively). Data from ECR of subject DMW and FCR of subject RJW. Plot symbols: *-facilitatory bias (bias and step have same sign), o-zero bias, x-inhibitory bias (bias and step have opposite sign). Regression lines labeled with values of bias in kgm.

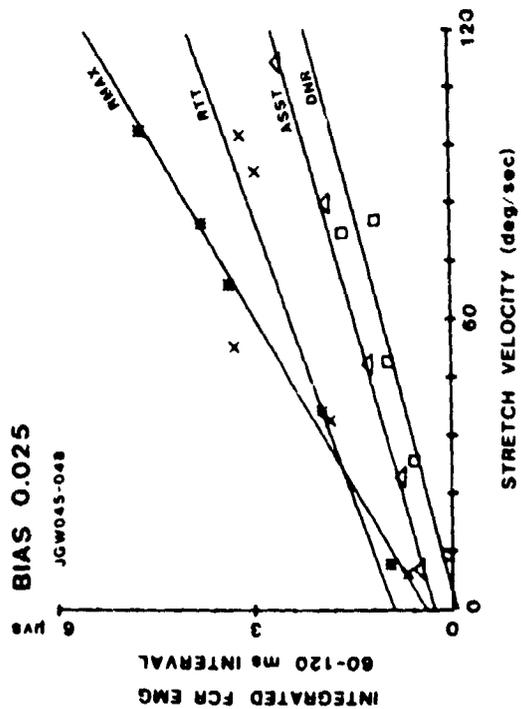
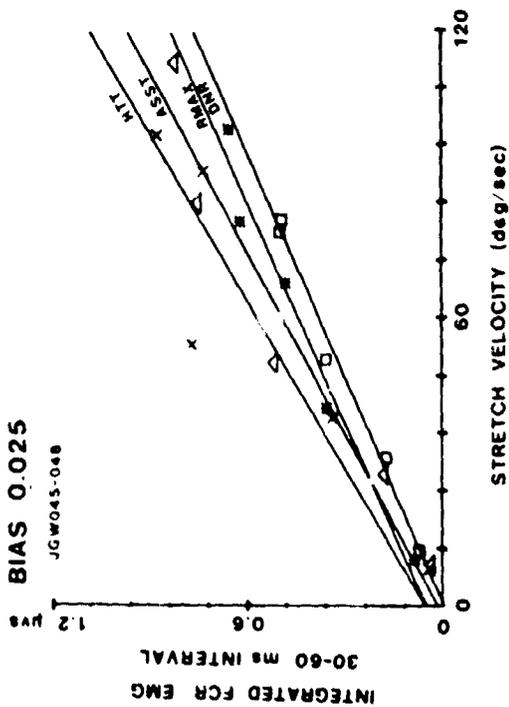
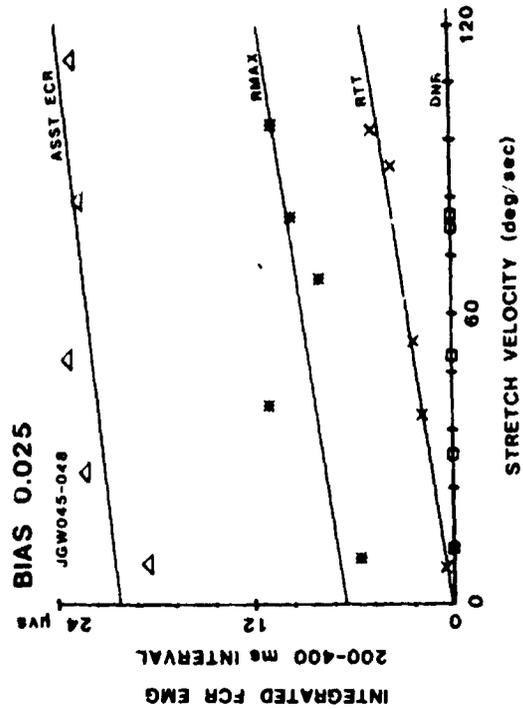
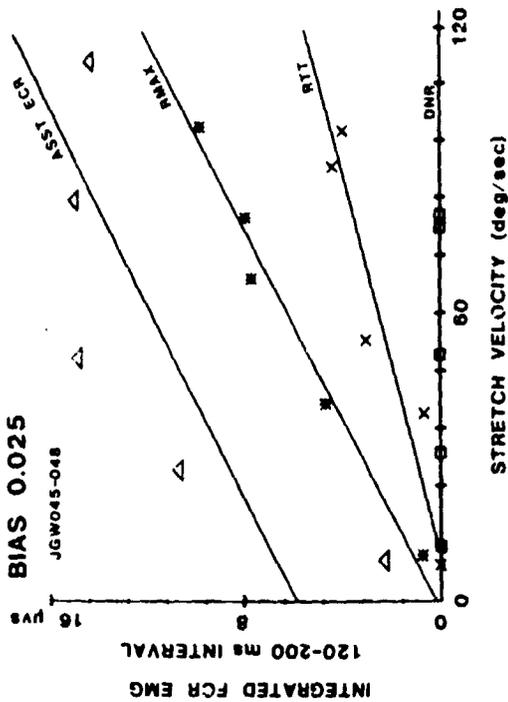


Figure 6: Gain plots for all intervals showing effects of instruction. Data from FCR of subject JGW. Plot symbols: x-RMAX, ^-ASST, o-DNR. Note that ASST data for 120-200 and 200-400 ms intervals is from ECR.

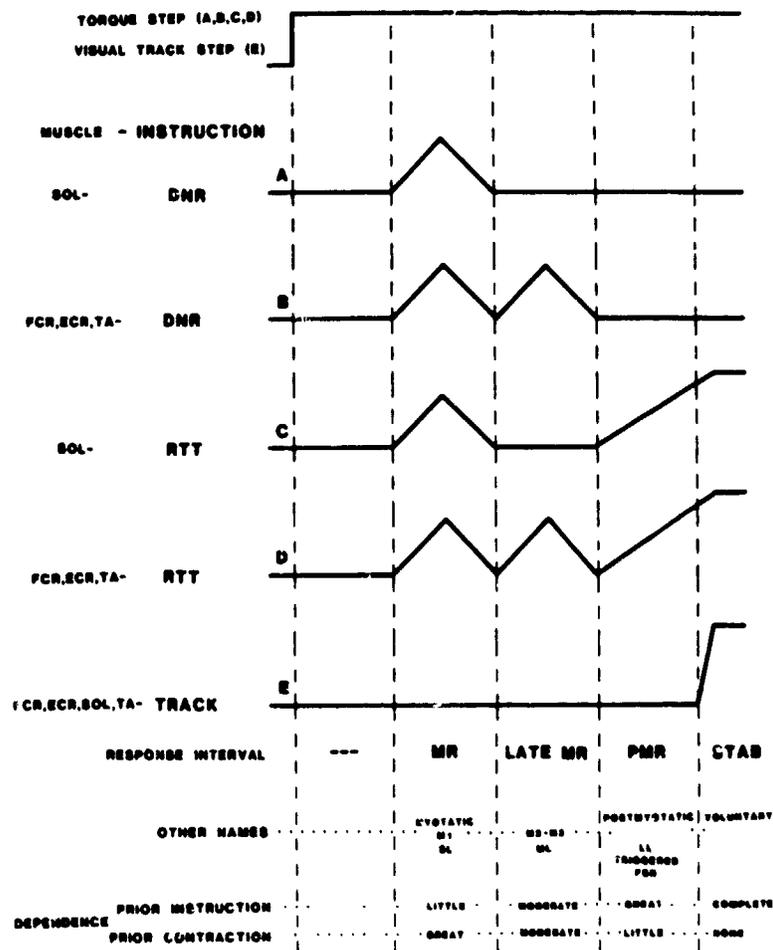


Figure 7: Generalized scheme for the classification of EMG responses to various stimuli. Step trace (top) represents step torque perturbation for EMG responses in traces A, B, C, and D, and visual step tracing stimuli for EMG response in trace E. Abbreviations: RTT-react to target, RMAX-react maximally, DNR- do not react, ASST-assist, SOL-soleus, FCR-flexor carpi radialis, ECR extensor carpi radialis, MR-myotatic response, PMR-postmyotatic response, STAB- stabilizing response. See text for abbreviations of other names. Time scale arbitrary.