ELECTROMYOGRAPHIC RESPONSE TO PSEUDO-RANDOM TORQUE DISTURBANCES OF HUMAN FOREARM POSITION

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Abstract—Pseudo-random torque disturbances applied to the human forearm permitted the identification of linear relationships between motion and biceps/triceps electromyographic activity. In particular, a weighted sum of position, velocity and acceleration provided an adequate description of electromyographic activity over a large range of disturbance amplitudes. While the velocity term was dominant when the subject was asked to resist the applied torque, the position term was of equal importance when the subject did not resist the torque.

The results support the concept of a continuous feedback control mechanism with adaptive properties.

RECENT investigations (CRAGO, HOUK & HASAN, 1976; DEWHURST, 1967; DUFRESNE, GURFINKEL, SOECHTING & TERZUOLO, 1978; DUFRESNE, 1977; MONSTER, 1973; NICHOLS & HOUK, 1976; WIENEKE & DENIER VAN DER GON, 1974) have examined the changes in motor output caused by pulses and steps of torque. Nonlinear features are clearly present in these data. They have been suggested to depend in part on receptor and motoneuron properties which are emphasized by the sharp transitions of torque amplitude (CRAGO *et al.*, 1976; DUFRESNE, 1977; MONSTER, 1973; NICHOLS & HOUK, 1976). Since this is not the most common occurrence in the course of physiological events, it seems desirable to minimize the effects due to such nonlinearities in order to focus first upon the main features of the mechanisms involved in the control of position. In so doing, one can also answer a second question: Are these features different from those used for the control of ongoing movements? The latter have been previously studied using ballistically-initiated movements (SOECHTING, 1973; TERZUOLO & VIVIANI, 1973; VIVIANI & TERZUOLO, 1973).

Pseudo-random torque sequences, that is, trains of flexion and extension torque pulses with random-like properties, are particularly attractive for the stated purposes since:

(a) the pulses are imposed on varying background levels of receptor and motor activities, and therefore can be expected to modulate more smoothly both the receptor and motoneuron outputs;

(b) noise (activity unrelated to the applied disturbance) can be suppressed by averaging;

(c) the cross-correlation between applied perturbations, angular displacement and electromyographic (EMG) activity provides all the information needed. Also a comparison can be made with the impulse responses to simple torque pulses;

(d) it can be verified whether or not such impulse responses change as a function of time (during the

sequence) or as a consequence of other experimental conditions (instructions to the subject, joint angle, mean muscle tension, etc.). The term 'operating point' will be used to denote this set of conditions;

(e) the subject cannot anticipate, in the course of the sequence, the direction of the applied torque perturbation.

EXPERIMENTAL PROCEDURES

Experimental set-up

Human subjects were seated in a straight-backed chair with their right forearm clamped in a fiberglass mold, the hand fully supinated. The elbow joint was aligned with the axis of a DC torque motor (Inland Motors model T-10042B). Angular position and acceleration, respectively, were obtained from a potentiometer mounted on the motor shaft and an accelerometer attached to the mold. EMG activity was recorded differentially from small surface electrodes over the biceps and triceps muscles with respect to an indifferent electrode placed on the left wrist. The bandpass of the amplifier extended from 50 to 1 KHz.

Data acquisition and torque-motor control were performed on-line by a digital computer. Biceps and triceps EMG activity was sampled at 5 ms intervals and full-wave rectified (without filtering). Note that by full-wave rectification one recovers the low frequency components of the EMG transients, thus providing an effective bandwidth of the sampled data from 0 to 200 Hz. Thus the low frequency components describing the motor units firing rate (DELUCA, 1975) will be contained in the ensemble averages. These were computed using the EMG data from 10 trials.

Shaft torque, motor current, angular position, and angular acceleration were sampled at half the EMG frequency. Angular velocity was obtained by numerical differentiation of the position data.

The input to the torque motor consisted of a slow ramp to a plateau of torque, followed by three consecutive pseudo-random sequences and a ramp back to a zero-torque level. The duration of the plateau was randomly varied from 2 to 4 s to permit the subject to adapt to a constant torque while preventing a precise anticipation of the start of the pseudo-random sequences. Torque excursions during the sequences were always centered with respect to the plateau torque level.

Abbreviation: EMG, electromyograph(ic).

The sequences were generated according to procedures described by DAVIES (1970) and PETERSON (1961). They consisted of trains of flexion and extension pulses, of constant amplitude, whose duration was randomly varied from 20 to 140 ms in integer multiples of 20 ms. Each sequence had a duration of 2.54 s. Three consecutive sequences were used to permit a check of nonstationarity. Thus, each trial lasted about 8 s. Three sequence amplitudes (8, 16 and 24 N·m) were chosen to cover the range of load changes the subject could comfortably resist. More details are provided elsewhere (DUFRESNE, 1977; O'LEARY & HONRUBIA, 1975; PONTE & PURVES, 1974).

Data analysis

A linear analysis of the experimental data was performed by several methods. Nonparametric models were obtained first by computing the cross-correlation between motor current and biceps EMG activity, triceps EMG activity, and angular position. The mean level of all variables and often a linear drift component as well, were removed prior to this computation (DAVIES, 1970). Two sets of correlation functions were obtained: series I (from the first two sequences) and series II (from the last two sequences). Each correlation function was scaled to obtain estimates of the impulse response functions for the three output variables (BRIGGS, GODFREY & HAMMOND, 1967). The following transfer functions were obtained by means of the Fast Fourier Transform: (1) motor torque to position, (2) position to biceps EMG, and (3) position to triceps EMG.

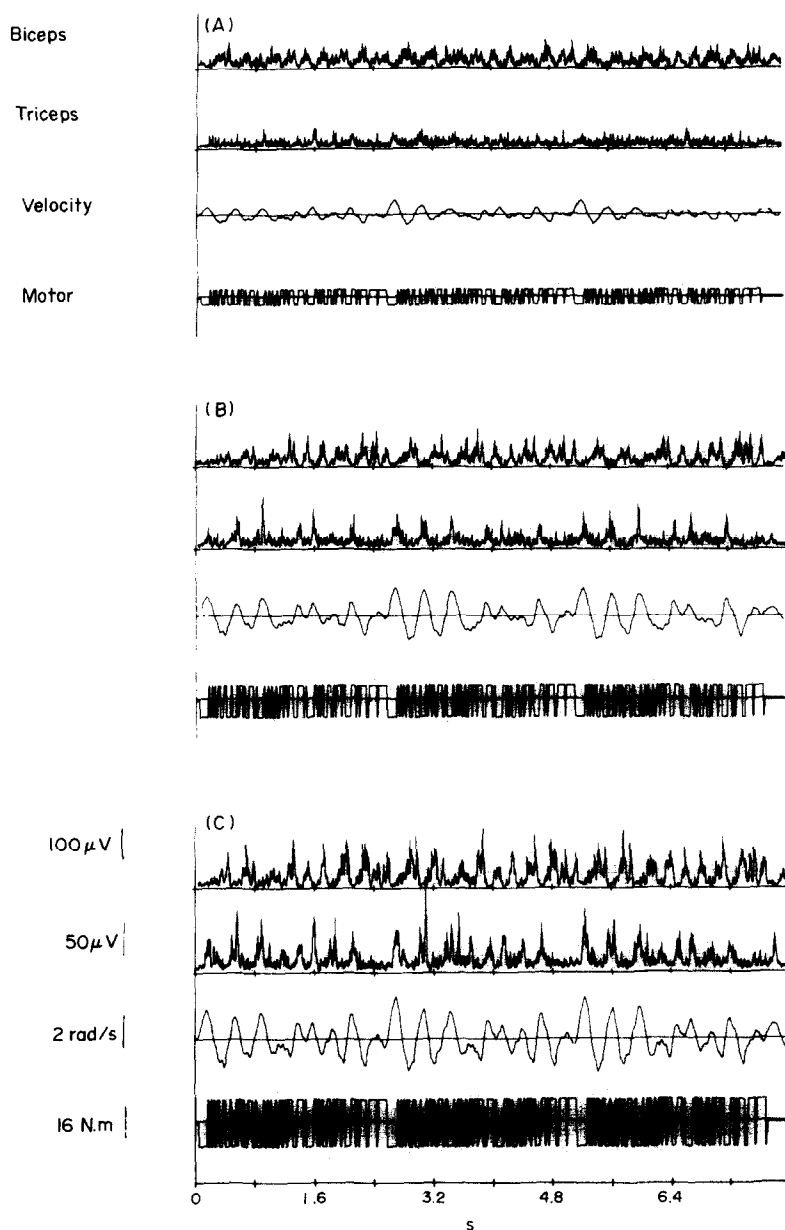A simplex algorithm (NELDER & MEAD, 1964) was

FIG. 1. Ensemble-averaged responses to pseudo-random torques with different amplitudes. Biceps and triceps EMG activity are shown together with the angular velocity of the elbow and the applied motor torque. The torque amplitude increases from 8 N·m (A) to 16 N·m (B) and 24 N·m (C). Each record represents the average of 10 trials for a single experiment.

applied to these transfer functions to obtain simple parametric models relating EMG activity to position and its low-order derivatives:

$$EMG(t) = Ap(t - D) + B\dot{p}(t - D) + C\ddot{p}(t - D). \quad (1)$$

The simplex method is a least-squares procedure to fit the transfer function data at 15 different frequencies between 0.5 and 15 Hz, using an equivalence of a 1 degree phase error to a 0.2 dB gain error.

RESULTS

The linear dependence of angular position and EMG activity on applied torque

In order to demonstrate a linear relationship between continuous torque disturbances and the kinematic and EMG variables, two points must be established. First, it must be shown that the impulse response functions used to describe these relationships do not depend on the exact sequence used. Second, it must be demonstrated that the impulse response functions provide an adequate description of the EMG and kinematic variables. If these points can be established, then these impulse response functions can be used to predict the response to any arbitrary disturbance.

To establish the first point, three torque sequences were used to test for a dependence of the impulse response functions on the magnitude and time-course of the applied torque disturbance. Figure 1 shows ensemble averages obtained with one of these sequences, whose amplitude was progressively increased from A to C. Note that in each record, the same sequence was presented three times in succession.

In this figure, the average biceps and triceps EMG activity appears to be somewhat noisy. Nevertheless, a marked reciprocity and modulation of activity is evident. Also, the angular velocity shows a substantial damping of the torque disturbance by the overall mechanical system. Moreover, there is a progressive increase in the modulation of the EMG activity and velocity [in 1(A–C)] which is roughly proportional to the increase in amplitude of the pseudo-random sequence. Finally, the bursts of the EMG activity which can be most clearly distinguished appear to be correlated with large-amplitude changes in velocity during stretching of the given muscle.

These relationships between the input and output variables can be more readily appreciated by comparing the corresponding impulse response functions obtained by cross-correlation (see Methods). Figure 2 presents such impulse response functions for three different input–output pairs: motor torque to biceps EMG (R_{MB}), motor torque to triceps EMG (R_{MT}), and motor torque to position (R_{MP}). In 2(A, C and E), average impulse response functions obtained from 9 sets of ensemble averages (3 sequences at 3 amplitudes) are shown together with two traces indicating the average plus and minus one standard deviation.

They represent the average response to a 20 ms torque pulse. Qualitatively, they agree with the response to single torque pulses (DUFRESNE, 1977; MONSTER, 1973; WIENEKE & DENIER VAN DER GON, 1974). However, there are important differences in details which will be considered in the 'Discussion'.

The rather small variances imply that the impulse response functions are essentially independent of torque amplitude and of the exact pattern of torque variation, although there is some weak dependence of the EMG maxima on torque amplitude. Thus, the first point mentioned above has been satisfied. Note that the impulse response of the position is a damped oscillation and that biceps and triceps activity are reciprocally organized. All three of these variables are uncorrelated with the applied perturbation after about 500 ms. The relationship between the kinematic variables and EMG activity will be discussed when similar records are presented on an expanded time scale in Fig. 5.

The Fourier transforms of the impulse response functions presented in Figs 2(A, C and E) are shown in (B, D and F), respectively. The gain and phase of these plots represent the transfer functions between the externally-applied torque and biceps EMG [2(B)], triceps EMG [2(D)], and position [2(F)]. In all cases, the transfer function is reasonably independent of the pulse sequence chosen and its amplitude, over the frequency range of 0.5–8 Hz. The variation among the position transforms of Fig. 2(F) is particularly small (although the phase deviation becomes quite noticeable at frequencies above 6 Hz). Moreover, the transforms for the biceps and triceps EMG densities [Fig. 2(B and D)] are similar, except for a constant phase difference of about 180 degrees. Note also that above 3 Hz, the gain of the EMG transforms decreases much more slowly than that for angular position, their respective slopes being 10 and 40 dB per decade.

Since the linear behavior of the three output variables considered appears to be self-consistent, it becomes appropriate to determine the extent to which their impulse response functions can predict the actual response to applied torques. Figure 3 presents the results of a linear convolution of the average impulse response functions with one of the torque sequences used (16 N·m). Sections A, B and C of this figure show the input (motor current) together with the experimentally observed and the predicted (model) responses. The error between the measured and predicted values is also shown.

The adequacy of the linear model for predicting the EMG can be readily appreciated from Fig. 3(A and B). The power spectrum for the error of the model [shown in Fig. 3(D) for the biceps EMG] is essentially flat. This fact indicates that the experimental data are fitted by the model to within a Gaussian random variable. Also, the ability of the model to predict the low-frequency variations in EMG activity, which are functionally significant, is quite evident.
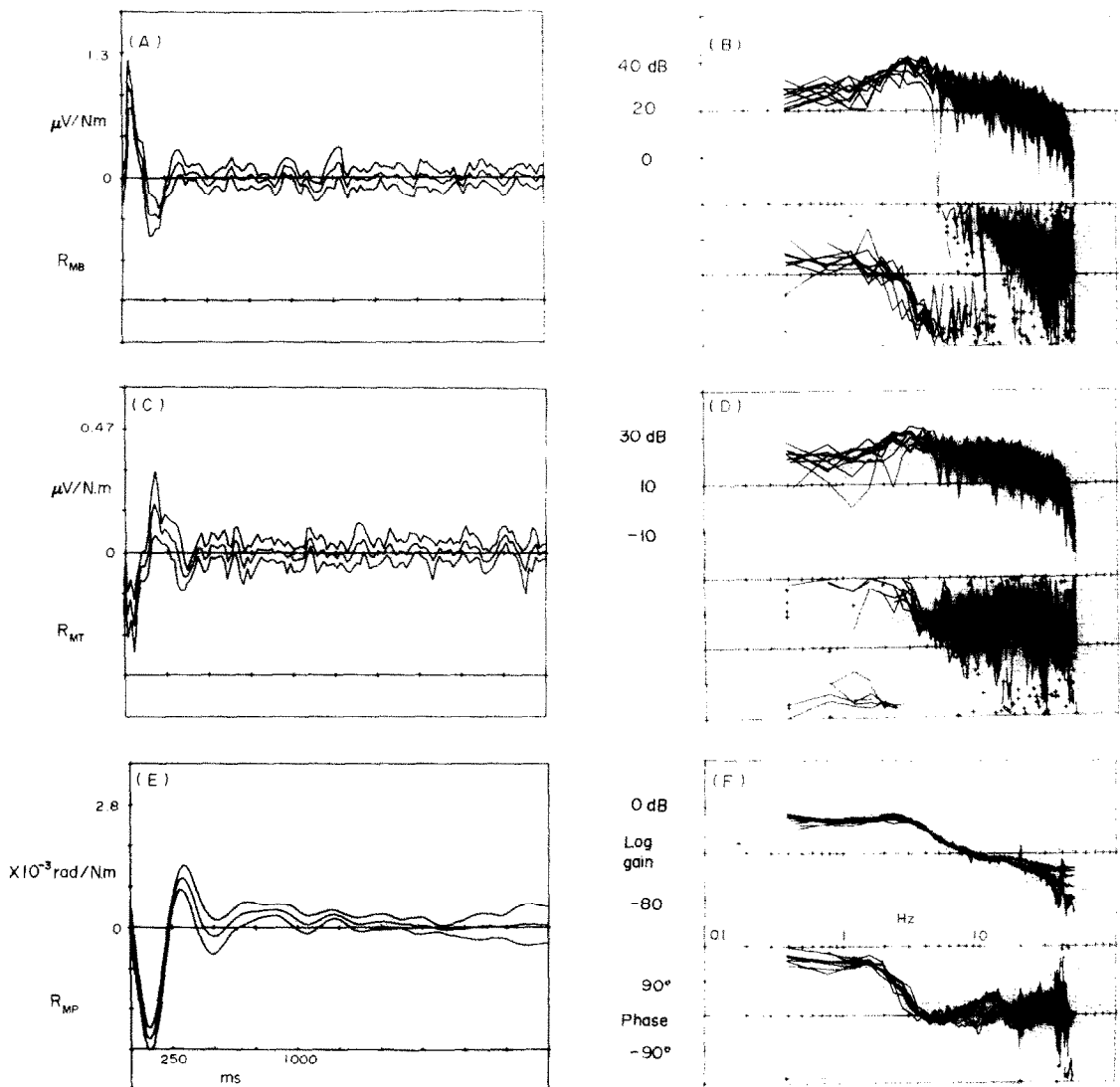
FIG. 2. Linearity of response to applied pseudo-random torques. The impulse response functions (R) relating motor torque (M) to biceps (B) and triceps (T) EMG activity and angular position (P) are presented in A, C, and E, respectively. Three traces give the mean of nine ensemble-averages (10 trials for each of 3 different maximal-length sequences and 3 sequence amplitudes from the experiment of Fig. 1), plus and minus one standard deviation. The Fast Fourier Transforms of these ensemble averages are shown overlain for biceps EMG (B), triceps EMG (D), and angular position (F).

Finally, the position impulse response function also provides a good visual fit to the actual data [Fig. 3(C)], although the error is quite pronounced near the resonance frequency of the forearm.

The dependence of EMG activity on the kinematic variables

The results presented in the preceding section as well as previous results (DUFRESNE, 1977; SOECHTING, 1973; SOECHTING, RANISH, PALMINTERI & TERZUOLO, 1976; VIVIANI & TERZUOLO, 1973) indicate that the EMG activity depends on the kinematic variables when a perturbation is applied. Therefore, as discussed under 'Experimental Procedures', a transfer function between position and EMG activity can be

obtained from the impulse response functions of Fig. 2. The light traces in Fig. 4 show this transfer function for one representative set of data. At low frequencies (below 4 Hz), the EMG activity is in phase with velocity. The rapidly increasing phase lag at higher frequencies suggests a significant time delay.

A parametric model, incorporating a dependence of EMG activity on position and its first two derivatives [equation 1], was fitted to the transfer function. Its behavior is given by the heavy traces in Fig. 4. The error of the fit is uniformly distributed over the frequency range of 0.3–20 Hz. Table 1 gives the values for the parameters of equation (1) for the experiments detailed in the previous section. L1, L2, and L3 correspond to torque sequence amplitudes of 8, 16 and
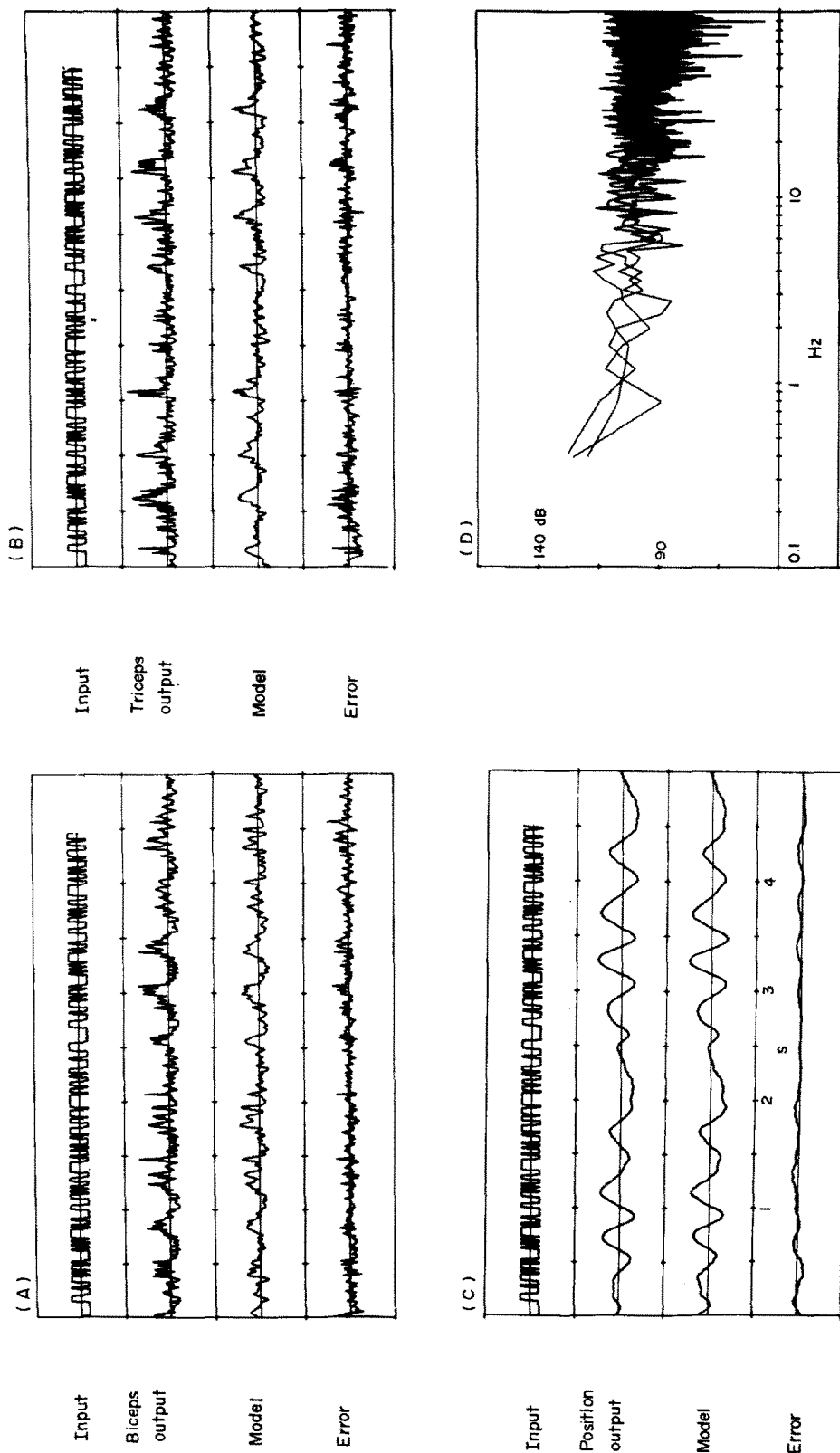
FIG. 3. Linear modeling of the EMG by convolution. The output predicted by the convolution of the impulse response functions of Fig. 2 with the input torque sequence is compared with actual records for the biceps EMG (A), triceps EMG (B), and forearm position (C). The subtracted error is shown for each variable. The overlaid traces of D give the power spectra for biceps EMG errors, obtained by using three different maximal length sequences as inputs for the linear model.
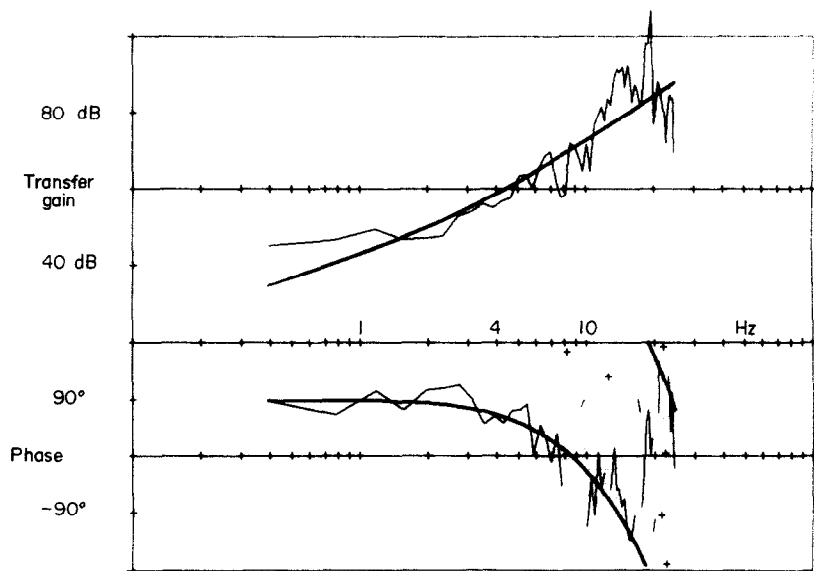
FIG. 4. Position-EMG transfer function for the biceps. The experimental transfer function, between position (taken as the input) and biceps EMG activity (output) is shown by the light traces. The transfer function of the 2nd order Fourier model is shown superimposed as the heavy traces.

24 N·m, while SI and SII denote the correlation series number (SI being the correlation calculated over 5 seconds at the onset of the perturbation, while SII was calculated over the final 5 s of the perturbation as described under 'Methods').

The values for coefficients A, B and C express the dependence of EMG density on position, velocity, and acceleration, respectively. When typical values for the kinematic variables (± 0.1 rad for position, ± 2 rad/s for velocity, and ± 40 rad/s^2 for acceleration) are entered in the equation of Table 1, the dependence

of the motor output on velocity and acceleration clearly outweighs its dependence on position. The mean value for the time delay (D) which provided the best fit was 47 ms. These values were consistent for each correlation series. Nonstationarity of this relationship (as expressed by changes in these constants from series I to II) will be discussed in the next section.

The stationarity of the linear model

Since the torque disturbance lasted over 7.5 s, the

TABLE 1. PARAMETERS FOR THE EMG MODEL:
EMG (t) = Ap (t − D) + Bṗ (t − D) + Cp̈ (t − D)

	A position (μV/rad)	B velocity (μV-s/rad)	C acceleration (μV-s^2/rad)	B/A (s)	C/A (s^2)	D (s)
	(A) Biceps					
L1 SI	71.6	14.8	0.759	0.207	0.0106	0.037
L1 SII	18.6	10.6	1.084	0.566	0.0581	0.060
L2 SI	60.3	11.7	0.566	0.194	0.0094	0.042
L2 SII	14.3	13.6	0.589	0.955	0.0411	0.059
L3 SI	81.3	14.3	0.626	0.176	0.0077	0.046
L3 SII	18.4	13.6	0.527	0.740	0.0286	0.059
	(B) Triceps					
L1 SI	23.2	4.45	0.160	0.192	0.0069	0.018
L1 SII	35.9	5.53	0.269	0.154	0.0074	0.038
L2 SI	20.4	5.23	0.237	0.256	0.0116	0.040
L2 SII	21.9	4.79	0.265	0.219	0.0121	0.050
L3 SI	27.9	6.30	0.382	0.226	0.0137	0.059
L3 SII	29.5	6.11	0.313	0.207	0.0106	0.050

Experimentally-determined parameters for the EMG model of equation (1). For each muscle, the first three columns give the coefficients of the model which express the dependence of the EMG on particular kinematic variables. The fourth and fifth columns provide ratios of these coefficients (B/A and C/A) while the last column gives the input delay time (D) for the best fit. Each row gives values for a particular torque sequence amplitude (L1–L3) and correlation series (SI or SII) (see text for additional details).
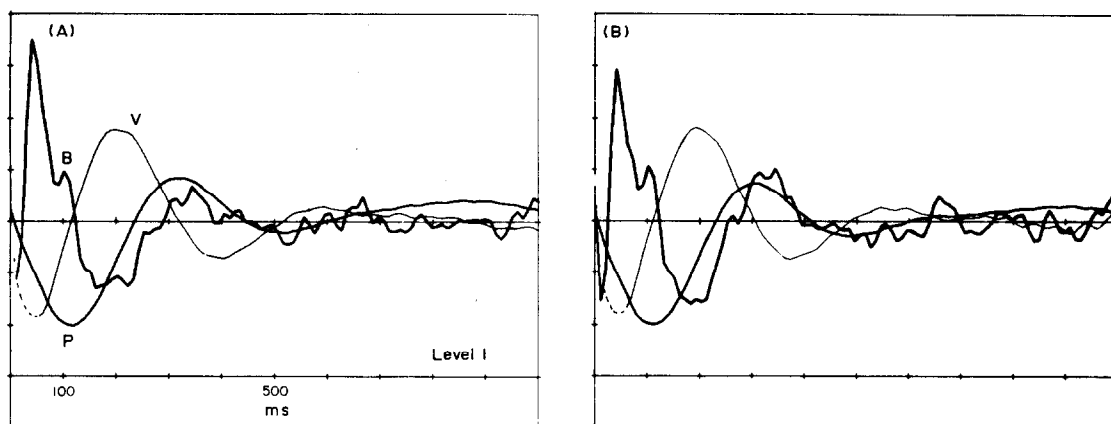
FIG. 5. Nonstationarity of the biceps EMG impulse response function. The biceps (B), position (P) and velocity (V) impulse response functions are shown as calculated over the first 5 s of the applied disturbance in A (series I) and the last 5 s in B (series II).

possibility of adaptation to the applied perturbation should be considered. Therefore, the possible dependence of the impulse response functions on time, relative to the onset of the torque disturbance, will be examined. Using the two sets of impulse response functions (series I and II), it is possible to demonstrate the existence of slow nonstationarities in the EMG response to applied torques.

The data of Table 1(A) show that the position sensitivity of the biceps decreased by a considerable amount over a time interval of one sequence length (about 2.5 s). However, there were no changes in velocity or acceleration sensitivity. For this particular experiment, the impulse response functions for the biceps were plotted on an expanded time scale, together with the position impulse response function and its first derivative. Figure 5 shows a pair of such plots. The position and velocity traces are labeled P and V, respectively.

Although both in 5(A) (series I) and in Fig. 5(B) (series II) the maxima and minima of the biceps activity coincide with the minima and maxima of the velocity, the initial rise of the biceps impulse response function is smaller for series II than for series I. The subsequent negative peak of the biceps impulse response function, however, is greater for series II. Such changes are compatible with the decline in position sensitivity shown by the modeling results of Table 1(A). Such a decline was observed in almost every case for the biceps EMG, but only infrequently for the triceps EMG.

Dependence of the EMG responses on the mean level of external torque

By imposing constant loading torques, one can investigate whether or not the response dynamics depend on the mean levels of motor output. To achieve this aim, experiments were performed in which the mean level of torque had non-zero values of ± 8 and ± 16 N · m (see 'Experimental Procedures').

The amplitude of the torque sequence was 16 N·m. Representative averages are shown in Fig. 6.

The mechanical variables are generally unaffected by the static torque level, although small d.c. shifts and slow base-line drifts can be observed. However, the mean level of biceps and triceps activity clearly depend on the mean level of applied torque, that of biceps being largest for the 16 N·m imposed extension torque [Fig. 6(A)]. Furthermore, the amplitude of the modulation of both triceps and biceps EMG activity increased in parallel with their mean level of activity. This trend is more clearly evident in Fig. 7, where the impulse response functions for the biceps and triceps EMG are shown for five different levels of d.c. torque. The left-hand part of this figure shows that the magnitude of the biceps impulse response function depends on the level of the imposed d.c. torque. Note also that these functions become increasingly periodic at the higher levels of imposed extension torque which increasingly loaded the biceps muscle. This periodic component has a frequency of about 3 Hz. The impulse response function for position also becomes more periodic (at the same frequency) as the mean level of torque increases. This effect is therefore due to the increase in muscle stiffness which parallels increases in the mean level of EMG activity.

In a similar, but reciprocal fashion, the amplitude of the triceps impulse response function also depends continuously on the static level of torque (right-hand side of Fig. 7). Note also that the triceps EMG ultimately becomes uncorrelated with respect to the applied torque as this muscle becomes increasingly unloaded.

In summary, the overall sensitivity (gain) of the changes in motor output to applied torques increases as the mean level of EMG activity increases. This might not be unexpected, because of the increased excitability of the motoneuron pool (GRANIT, 1970). Also, it has already been qualitatively described by
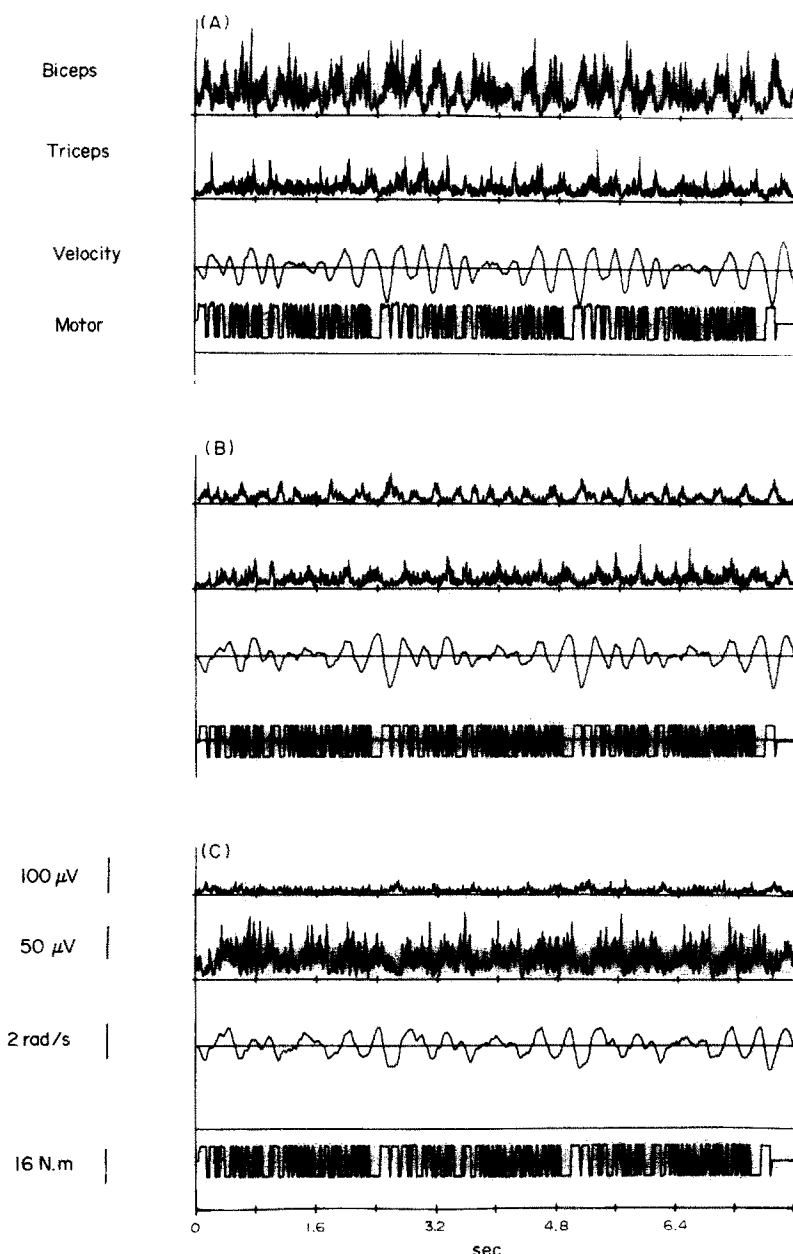
FIG. 6. Dependence of biceps and triceps EMG responses on the level of static torque. The format is that of Fig. 1, showing the responses to 16 N·m torque sequences at zero mean level of torque (B) and in the presence of 16 N·m relative extension (A) and flexion (C) torques.

previous investigators (MARSDEN, MERTON & MORTON, 1972).

One more point is noteworthy. The increased drive to alpha motoneurons could be accompanied by changes in gamma motoneuron drive, and consequently in muscle spindle dynamic sensitivity. Indeed, if the ratio between fusimotor static and dynamic actions upon the muscle spindles were to change, the sensitivity of these receptors to position and velocity parameters would also change (CHEN & POPPELE, 1978; CROWE & MATTHEWS, 1964; HULLIGER, MATTHEWS & NOTH, 1977). Since this aspect is highly significant from a functional viewpoint, it was pursued

quantitatively. To this end one should note that the net result of changes in the impulse response functions for the EMG and kinematic data can be expressed in terms of sensitivity constants for the parametric Fourier models. From this point of view, the position sensitivity of the triceps EMG for the experiment of Figs 6 and 7 shows a 100-fold drop as the mean muscle tension decreases (from d.c. levels of 8 N·m relative flexion to 16 N·m relative extension). The velocity and acceleration sensitivities also decrease, but only by a factor of 20, over the same range. Thus the dynamic sensitivity of the triceps EMG was increased *relative* to the static (position)
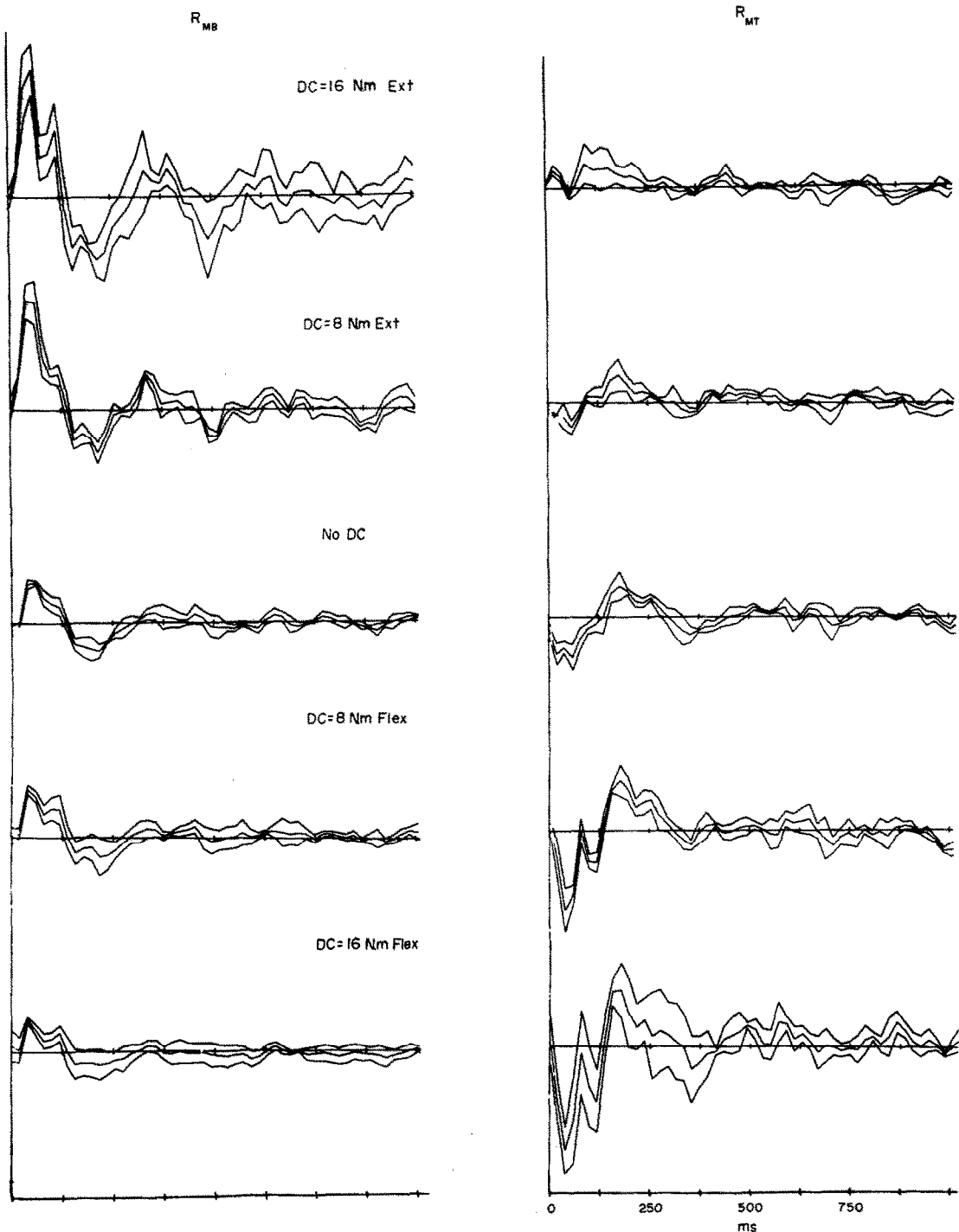
FIG. 7. Dependence of EMG impulse response functions on the static torque level. Biceps (R_{MB}) and triceps (R_{MT}) impulse response functions are shown for five levels of static torque. Each set of three curves indicates the mean response amplitude, plus and minus one standard deviation, from a set of three ensemble averages (3 averages of 10 trials each). Impulses response functions for a given muscle are plotted at the same absolute scale.

sensitivity when the triceps was unloaded. A similar, but weaker trend, was also observed for the biceps EMG. The conclusion is consistent with the results of VALLBO (1970) regarding changes in static fusimotor activity during intentional muscle contraction, and the subject will be considered in more detail in the discussion.

Changes in the dynamic response as a function of joint angle

Changes in joint angle are known to affect the torque developed by the biceps and triceps muscles (BOUISSET, 1973). Therefore, experiments were performed to determine the influence of absolute joint
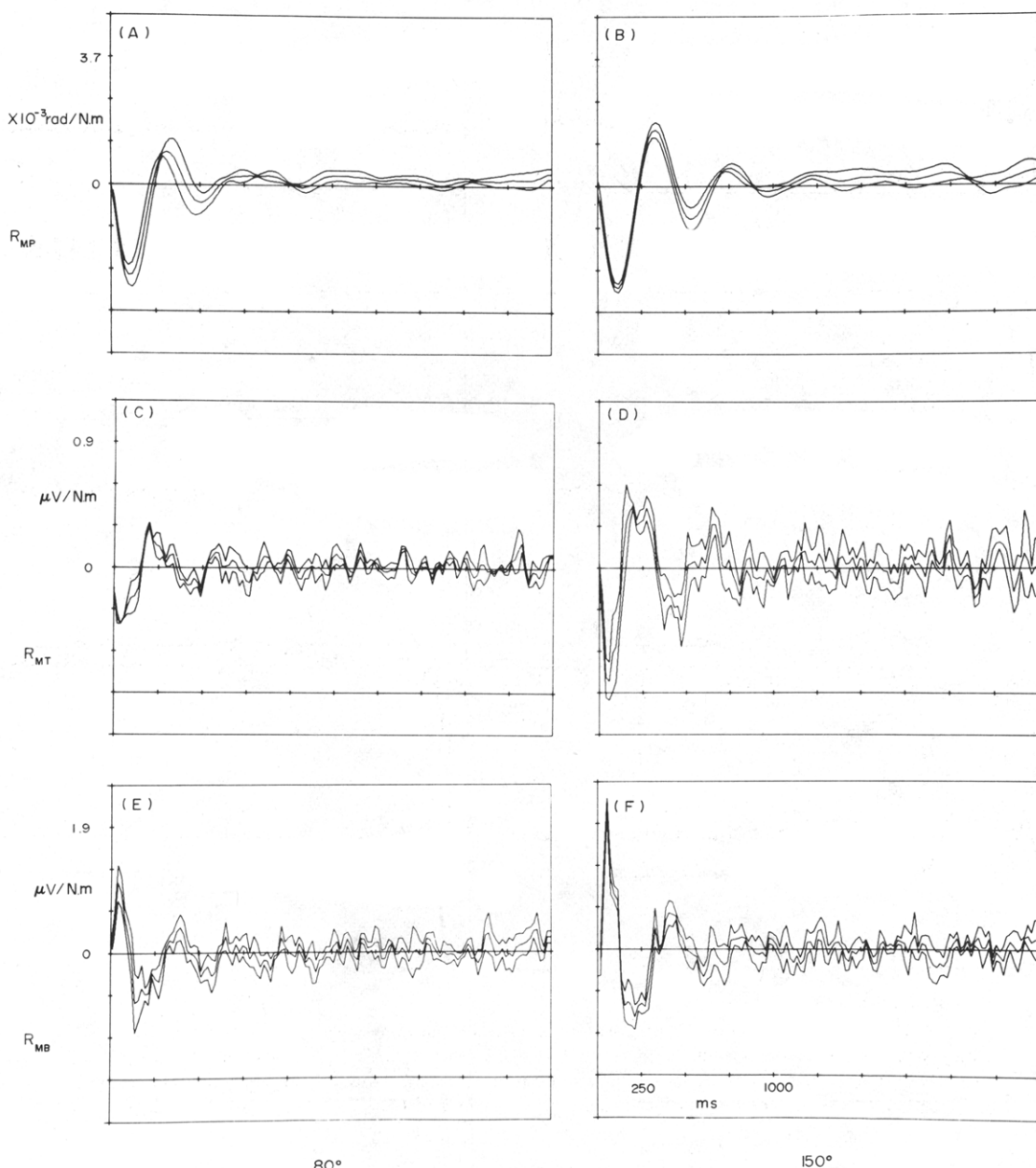
FIG. 8. Dependence of impulse response functions on mean forearm position. The data of parts A, C, and E were obtained at an angle of 80° while B, D, and F present those for an angle of 150°. A set of three ensemble averages provided the means and ranges of variation for each part of this figure.

angle on the impulse response functions for the EMG and position. Figure 8 shows these functions for two extreme positions of the elbow: 80 degrees (maximal flexion) and 150 degrees (maximal extension). Figure 8(A and B) show that the position impulse response function becomes highly oscillatory near maximum extension. The corresponding Fourier transforms showed that this oscillation occurred at the resonant frequency of the forearm. Nonetheless, the peak amplitude of the position response function was not greatly altered by a change in mean joint angle. Figure 8(C and D) show that the magnitude of the

EMG impulse response functions becomes significantly larger as the forearm is extended. However, little change in magnitude can be detected over the angular range of 75–120 degrees.

Dependence of the dynamic response on the instruction given to the subject

In all experiments considered so far, the subject was instructed actively to resist the applied perturbation by attempting to maintain constant the position of his forearm. The resulting EMG density was then
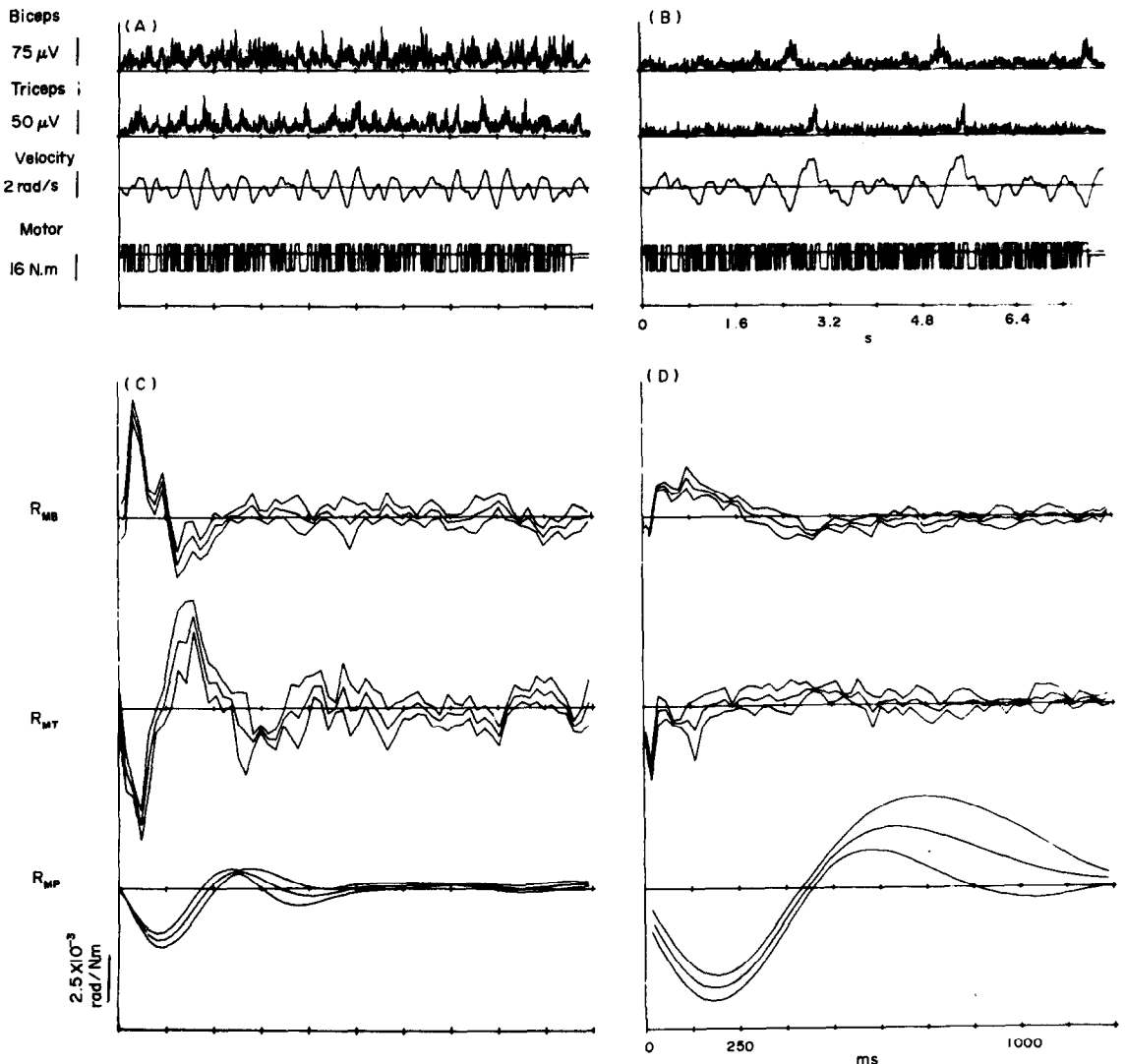
FIG. 9. Dependence of pseudo-random torque responses on the given instruction. The ensemble-averages were obtained from experiments in which the subject was instructed to oppose (A) or not oppose (B). The impulse response functions obtained from the data of A and B are presented in C and D, respectively, using the conventions of Figs 2 and 8.

smoothly modulated about a significant mean level of activity. When the subject was asked instead not to resist the applied torque disturbances, the resulting impulse response functions changed greatly.

Figure 9 compares the data from experiments in which the subject was instructed to resist or not resist the applied torques (left and right part of the figure, respectively). When the subject is instructed not to resist the mean level of activity is much smaller; its modulation by the applied torque is also smaller and less structured (see also EVARTS & TANJI, 1974; HAMMOND, 1956). Moreover, the effective stiffness of the forearm is decreased since the amplitude of the oscillation increases while its frequency decreases (C and D).

More importantly, the motor output response is greatly reduced despite the fact that the amplitude

of the changes in position increased. Furthermore, EMG activity is much more closely related to position than to velocity. Whereas the maximal EMG activity coincides with peak velocity (Fig. 5) when the subject actively resists the perturbation, it is delayed and occurs much closer to the peak displacement when the subject does not resist the perturbation. This observation was confirmed by a frequency analysis of the data. The phase between position and EMG activity is indeed much lower, never approaching 90 degrees (as in Fig. 4) and being negative at frequencies above 4 Hz.

DISCUSSION

The results we have presented demonstrate (1) that pseudo-random sequences can be used successfully to characterize the changes in motor output caused by

load perturbations; (2) that such changes in motor output are related to and depend upon the kinematic variables in a reasonably linear manner; and (3) that the motor output response depends primarily on the angular velocity when the subject intentionally resists the applied load perturbation.

Points (2) and (3) are in agreement with previous findings (SOECHTING, 1973; SOECHTING et al., 1976; TERZUOLO & VIVIANI, 1973; VIVIANI & TERZUOLO, 1973) obtained from studies on the control of ballistically-initiated movements, suggesting that the same control system provides for position control and for the control of ongoing movements. In particular, in both instances flexor and extensor EMG activity is reciprocally organized. The quantitative relationship between position and EMG activity, as expressed by the transfer function between these variables, is virtually superimposable under these two experimental conditions. Furthermore, in one experiment we reduced the inertial load by a factor of two and found that the transfer function remained the same even though the impulse response functions for position and EMG activity were substantially affected. This finding is also in agreement with results obtained during ballistically-initiated movements. Thus, we feel that our conclusion is warranted, and we shall not pursue the point further.

We shall now focus upon the following points: (1) a comparison of the EMG response to single torque pulses and to pseudo-random sequences of such pulses and (2) the dependence of the response dynamics upon the operating point, as we have defined it in the 'Introduction'.

The similarities between the EMG response to a single pulse of torque and the impulse response functions presented here (cf. Figs 2 and 5) can be summarized as follows: in both instances, there is a short latency increase in EMG activity (about 20 ms), followed by an abrupt decrease. Also, the amplitude of the response is correlated with the amplitude of the velocity (DUFRESNE, 1977; MONSTER, 1973). However, a more detailed examination reveals major differences. First of all, the duration of the initial burst of EMG activity of the stretched muscle in response to a single pulse of torque is largely independent of pulse duration, although the time course of the velocity is obviously affected by this parameter (its peak being delayed by increasing the pulse duration). In contrast, the impulse response functions obtained by using pseudo-random sequences clearly follow the time course of the angular velocity, becoming negative when the velocity reverses sign (Fig. 5). Secondly, the burst of activity caused by a single torque pulse is known to have two peaks with fixed latencies (cf. CONRAD, MEYER-LOHMANN, MATSUNAMI & BROOKS, 1975; DUFRESNE, 1977; EVARTS & TANJI, 1974; LEE & TATTON, 1975), whereas the impulse response is less clearly subdivided. Its second peak is much smaller and has a longer latency (about 100–120 ms). Since the presence of this peak at a fixed latency is

considered to be crucial evidence for the contribution of transcortical reflex loops to the response (EVARTS & TANJI, 1974; LEE & TATTON, 1975), our data suggest that this problem deserves further consideration (cf. also GHEZ & SHINODA, 1977).

Finally, one should note that the input-output relationship between position and motor output obtained by using pseudo-random torque sequences is remarkably similar to that which describes the linear component of the behavior of muscle spindle receptors to stretch (POPPELE & BOWMAN, 1970; ROSENTHAL, McKEAN, ROBERTS & TERZUOLO, 1970). In contrast, the response to single torque pulses exhibits a much greater acceleration sensitivity (DUFRESNE, 1977).

More generally, the experimental results and the results of modeling presented in this paper are in agreement with the premise upon which the experiments were designed, namely that the use of pseudo-random torque sequences would tend to reduce the influence of alpha-motoneuron and spindle nonlinearities, which are present in the motor output responses to single torque pulses. Therefore, it is our view that the features which are peculiar to the motor output response to single torque pulses are less relevant to the general question of how movements are controlled by central mechanisms, but rather reflect the nonlinearities mentioned above.

The final point which will be considered is the dependence of the reflex gain and dynamics on the operating point of the system. The results have shown that although the impulse response functions obtained at different operating points are basically similar, changes in gain and dynamics are introduced by changing the mean level of motor activity, the mean angular position and the task (as specified by the instructions given to the subject). Moreover, these data also indicate the presence of a slowly adaptive behavior by the system.

All these findings are readily compatible with the involvement of a functionally simple feedback system, the parameters of which can vary, that is, an adaptive control system (BERNSTEIN, 1967; GREENE, 1972). Regarding the physiological substrates of such an adaptive control system, central biasing actions upon segmental reflex loops (GRANIT, 1970; LUNDBERG, 1975) provide the simplest such mechanism consistent with the experimental data. For example, our results showed an increase in gain and a relative decrease in velocity sensitivity as the mean level of EMG activity increased. Both changes may be ascribed to an increase in fusimotor static drive to muscle spindle as the rate of alpha-motoneuron activity is increased during intentional contraction, as was found by VALLBO (1977).

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