Journal of Physiology (1993), **469**, *pp.*673-691
With 8 *figures*

Printed in Great Britain

ORGANIZATION OF MOTOR OUTPUT IN SLOW FINGER MOVEMENTS IN MAN

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(*Received 13 April 1992*)

SUMMARY

1. Slow finger movements were analysed in normal human subjects with regard to kinematics and EMG activity of the long finger muscles. Surface EMG from the finger extensor and flexor muscles on the forearm was recorded along with angular position and angular velocity during voluntary ramp movements at single metacarpophalangeal joints. Angular acceleration was computed from the velocity record.

2. It was found that movements were not smooth but characterized by steps or discontinuities, often recurring at intervals of 100–125 ms, yielding velocity and acceleration profiles dominated by 8–10 Hz cycles. The discontinuities were manifest from the very first trial and thus not dependent on training. Their amplitude and amount varied between subjects but were relatively stable for the individual subject.

3. The 8–10 Hz cycles were seen with voluntary ramp movements of widely varying velocities, higher velocities being associated with larger steps recurring with the same repetition rate as the small steps of slow voluntary ramps. Maximal step amplitude observed was more than one order of magnitude larger than physiological tremor.

4. The individual 8–10 Hz cycle was asymmetrical in that decelerations usually reached higher peaks than the preceding acceleration, suggesting that the antagonist contributed with a braking action. Moreover, in very slow voluntary ramps, the movement cycles were often interspaced by periods of zero velocity, providing a highly non-sinusoidal velocity profile.

5. The EMG of the agonist and the antagonist muscles was modulated in close relation to the accelerations and decelerations respectively of the individual movement cycle. These modulations were present in both extensor and flexor muscles, although they were more consistent and usually more prominent in the former.

6. The findings indicate that a feature of slow finger movements was an 8–10 Hz periodic output to the muscular system, suggesting that slow finger movements are implemented by a series of biphasic force pulses, involving not only the shortening agonist muscle propelling the movement, but the antagonist muscle as well whose activity increased shortly after the agonist and contributed to a sharp deceleration of the individual step of movement.

7. It is proposed, as a hypothesis, that this biphasic motor output may reflect a similar organization of the descending motor command for slow finger movements.

Hence, this command would include a series of biphasic pulses, concatenated at a rate of 8–10 per second and a pulse–height regulator capable of setting the size of the pulse and thus the overall speed of the movement.

INTRODUCTION

It has been reported in passing that voluntary finger movements may be characterized by discontinuities which recur with a similar frequency as the oscillations of physiological tremor during position holding (Marshall & Walsh, 1956; Young & Hagbarth, 1980), although the phenomenon has not be the subject of systematic analysis.

Marshall & Walsh (1956) state that a tremor at 7–12 Hz 'was seen at the wrist, elbow, shoulder, ankle, knee, and hip' although 'it may be clearly recordable only during the course of movement.' Navas & Stark (1968) analysed supination–pronation movements of the forearm during visual tracking, and demonstrated, in passing, 8–10 Hz modulations of angular velocity when subjects strived to follow predictable track signals.

Discontinuities of lower repetition rate, on the other hand, have been demonstrated by several groups. Navas & Stark (1968) showed that 2·5 Hz 'saccades' dominate when subjects are tracking unpredictable visual targets, whereas Brooks (1974) distinguished between continuous and discontinuous movements at the elbow joint of the monkey. Both groups discussed intermittent feedback as an essential mechanism behind the low rate discontinuities. Finally, Abend, Bizzi & Morasso (1982) and Bock (1990) demonstrated discontinuities of low repetition rate in multi-joint movements.

The observation of 8–10 Hz discontinuities has loosely been taken to indicate that physiological tremor is more pronounced during movement than during position holding (Marshall & Walsh, 1956; Young & Hagbarth, 1980). However, it seems far from clear that the same mechanisms account for position tremor and discontinuities during movements.

The present study demonstrated that voluntary movements of slow or moderate speed at a single metacarpophalangeal joint are usually characterized by a series of prominent and robust discontinuities at 8–10 Hz. These discontinuities were associated with a pulsatile motor output which seemed to engage not only the agonist but the antagonist as well, respectively propelling and braking step movements.

The findings suggest the hypothesis that slow finger movements are implemented by a series of repetitive force pulses of the reciprocal muscles of the joint, each cycle comprising an agonist driving pulse which precedes an antagonist braking pulse by a few tens of milliseconds.

Preliminary reports of some of this work have been published previously (Vallbo & Wessberg, 1992, 1993).

METHODS

The experiments were performed on twenty-five volunteers, aged 21–41 years. In most runs the left hand was used. Two subjects were left-handed.

The informed consent of the voluntary subjects was obtained according to the Declaration of Helsinki (British Medical Journal (1964) 2, 177). This study was approved by the Ethical Committee of the Medical Faculty of the University of Göteborg.

General procedure and equipment

The subject was comfortably seated in a reclining chair with the left arm resting on a supporting platform. The hand was held with a clamp which permitted free finger movements, but prevented movements of the wrist, which was held in an intermediate position.

One finger of the left hand, usually the third, was strapped to a splint which permitted movements only at the metacarpophalangeal joint. The splint was attached to an actuator device by means of a low-mass hinged bar. The actuator has been described elsewhere (Hulliger, Nordh & Vallbo, 1982; Al-Falahe & Vallbo, 1988). Transducers of the actuator provided continuous recording of metacarpophalangeal joint angle, velocity, and torque. An integral servo-motor compensated for friction and inertia. Thus the actuator device normally presented zero load to the moving finger. The servo-motor was also used to generate constant torque loads of different sizes. In control experiments, other recording systems were used in order to ensure that the kinematic features of the voluntary movements were genuine and did not include artifacts generated by the servo-system, i.e. an infrared light-emitting diode system for angular displacement (Selspot, Selcom AB, Partille, Sweden) and an accelerometer.

An oscilloscope in front of the subject was used for visual tracking. One beam was swept vertically and split into two halves, the top half displaying the desired target and the bottom half the actual joint angle. Direct vision of the finger was obscured with a screen. A microcomputer was programmed to control the actuator, the tracking oscilloscope, and other equipment including a separate sampling computer (see below).

Recordings

EMG was recorded in sixteen subjects by means of surface electrodes. The electrodes were placed on the dorsal surface of the proximal forearm, over the area of maximal palpable contraction of the finger extensor muscles (m. extensor digitorum communis) and on the volar surface of the distal forearm where optimal EMG activity was obtained during finger flexion. The kinematic parameters and the torque were sampled at 400 Hz on-line on a microcomputer. EMG was root-mean-square rectified with rise and decay time constants of 1·6 ms and 4·8 ms respectively and then sampled at 800 Hz. An acceleration signal was derived off-line by differentiation of the angular velocity signal which was first low-pass filtered by a moving average procedure, yielding −3 dB cut-off at approximately 50 Hz and practically zero gain at 120 Hz.

Experimental protocol

The main experimental protocol comprised a visually guided tracking task, and a task when the subject was asked to reproduce as faithfully as possible the preceding tracking movement when visual information was denied (Fig. 1*A*). The subject was constantly urged to perform with maximal precision in both tasks. Each trial consisted of five phases, i.e. a position-holding phase, an extension movement of 20 deg, an inter-movement position-holding phase, a flexion movement back to the initial position, and finally a position-holding phase. Auditory cues prompted the subjects to begin to move. In the tracking movements, the target moved with a constant speed corresponding to 4, 10, 25 or 62 deg/s, starting 300 ms after the auditory cue. In the non-visual task, the target and the actual joint position were displayed for a few seconds initially, when the subject was asked to match the steady target position, and for a short period at the end of the sequence (Fig. 1*A*).

Training consisted of three to ten tracking movement sequences for each track speed, until the subject was adequately familiar with the procedure. Good performance in the non-visual task was usually obtained within just a few trials.

In some trials, a constant torque load, opposing the finger extensor muscles, was imposed on the finger. Loads of 1, 5, and 10 % of the maximum voluntary torque were used. Periodically, the subject was asked to perform the movement sequences with a varying degree of voluntary co-contraction of the finger flexor and extensor muscles.

In most trials, the third finger was used and the subject was asked not to move the other fingers concomitantly. The third finger was also kept separated from the neighbouring fingers by means of rubber band supports.

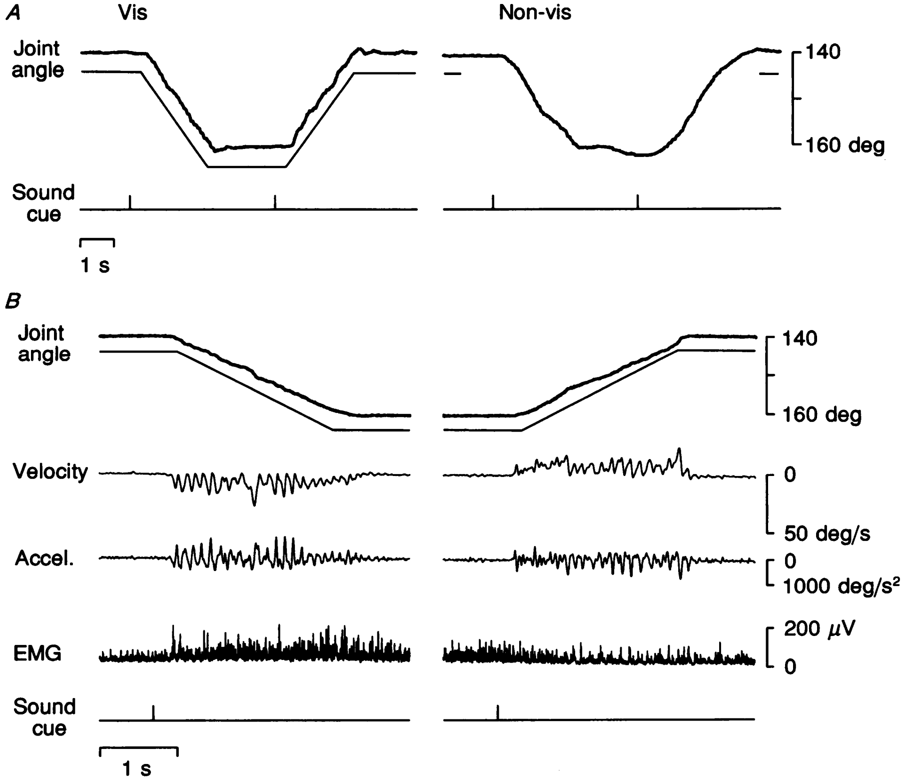

Fig. 1. Structure of standard test sequence and subject's performance. *A* shows sequence consisting of ramp-and-hold movements, one extension and one flexion, which were repeated twice, first in a direct tracking protocol (Vis) and then without visual control when the subject was asked to reproduce from his memory the movements previously performed (Non-vis). Records from above, subjects performance, tracking signal (slightly shifted downwards), and sound cues to prompt onset of movement. *B* shows subject's performance and EMG. The records show from above joint angle, track signal, angular velocity, angular acceleration, EMG activity, and sound cues to initiate movements. EMG rectified and root-mean-square filtered. Note that, extension movements, i.e. shortening of the muscle studied, are indicated downward in this and all other records. Angular position 180 deg corresponds to full extension.

Additional tests

Trials were also performed without adherence to the protocol procedure described above. These included self-paced movements of widely varying amplitudes and speeds. Five subjects were also asked to 'just move the finger a little' directly after being seated for the first time, i.e. without any prior instruction or description of the experiment or its intent whatsoever.

Trials were also performed with movements of the second, fourth, or fifth fingers, movements without the finger splint, and movements of all fingers in unison. Using the Selspot system, movements of fingers of the right hand were studied in four subjects.

Altogether more than 2500 voluntary movements were analysed.

Analysis

For all movements, the presence of periodicities at different frequencies was analysed using two different Fourier spectral analysis methods. A few words about the nature of the analysis and the properties of the two approaches may be helpful. The spectral content of a time series process is usually presented as a 'power' spectral density function, or power spectrum. Examples are shown in Figs 3–5. Each data point in the power spectrum represents a statistical estimate of the variance of the process within a narrow frequency band as indicated by the distance along the x-axis between the data points (Bendat & Piersol, 1986).

For a kinematic process, the position, velocity, and acceleration records contain, qualitatively, the same frequency information, but lower frequency components are greatly enhanced in the former (Halliday & Redfearn, 1956; Marshall & Walsh, 1956). In the present study we analysed the spectral content of the acceleration record rather than velocity or position records.

One approach for computation of the power spectral density functions was to use Fourier transforms of weighted overlapping data windows (Welch, 1967; Harris, 1978). Formally, this approach requires a random process with at least local stationarity, i.e. in our case, stationarity during the individual voluntary ramp. For a fair number of our trials, this assumption was dubious because non-stationarity seemed obvious to the naked eye. Hence, an alternative method was used as the main approach because it was less strict in requiring the assumption of stationarity. This method involved 'hard clipping' of the acceleration signal, implying that the signal only took instantaneous values of plus or minus unity depending on the original signal being positive or negative at the sample point. The autocorrelation function of this clipped signal was calculated, and scaled as prescribed. Finally, the Fourier transform was calculated from the modified auto-correlation (method described in Bendat & Piersol, 1986; Van Vleck & Middleton, 1966). Generally, the two methods provided very similar results. However, the power spectra illustrated in the present paper are all based on the latter method.

In our illustrations of power spectra (Figs 3–5) the y-axis represents percentage total variance of the acceleration. The frequency resolution of the power spectra is 1 Hz. Hence each data point represents the relative contribution of variance within the frequency band limited by the numeral indicated on the x-axis plus and minus 0·5 Hz. For a reduction of random error, all presented power spectra represent averages from at least forty-eight data strings. Two such strings were obtained from each voluntary ramp movement. All presented peaks were tested with the χ^2-distributed test appropriate for power-spectral data (Bendat & Piersol, 1986), and are statistically significant ($P < 0{\cdot}01$).

For the analysis of the relation of EMG to acceleration, a standard linear cross-correlation method was used. All computations were made using software developed by one of the authors, written in Borland Turbo Pascal for IBM PC-type computers.

RESULTS

The present study is focused on the finding that slow finger movements are not smooth but characterized by successive fluctuations in velocity. Examples are shown in Figs 1 and 2 from a test when the subjects strived to make smooth, ramp- shaped movements of the metacarpophalangeal joint of the third finger. Discontinuities are discernable in the record of the angular position but are more evident in the velocity record. It may be seen that modulations of the velocity often occurred at intervals of 100–125 ms, corresponding to a frequency of 8–10 Hz. The individual cycle in the velocity record reflected changes of angular position amounting to 0·3–2·5 deg, i.e. muscle length changes of 0·04–0·3 mm, in the sample records of Fig. 2. The discontinuities were inevitable in the sense that subjects were not able to produce movements without discontinuities however hard they tried.

The present analysis is focused on the 8–10 Hz cycles which dominated in most records. However, as illustrated in Figs 1 and 2 the voluntary ramps also contained discontinuities recurring with higher as well as lower frequencies, as will be described in more detail below.

Variability

The amount and the regularity of the 8–10 Hz periodicity were broadly similar between successive trials of an individual subject, whereas variations between subjects were more evident. The sample records of Fig. 2 are fairly representative of the inter-trial as well as inter-subject variation. In some subjects, the 8–10 Hz cycles were pronounced and dominated the velocity record in practically all movements (Fig. 2*A*) whereas other subjects produced more irregular movements which included larger amounts of discontinuities at other intervals (Fig. 2*B*). However, with all

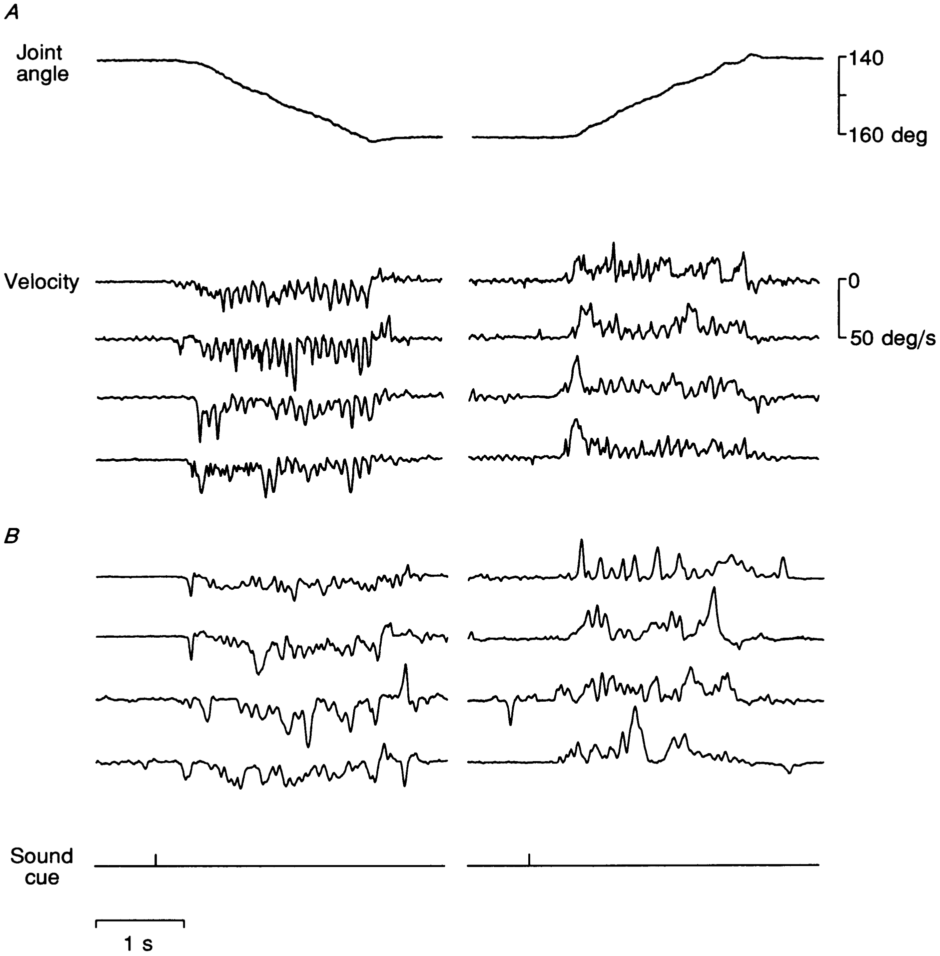

Fig. 2. Characteristics of precision movements at a single metacarpophalangeal joint from two different subjects, M.S. in *A* and A.P. in *B* (cf. Fig. 3). Subjects were asked to track ramp and hold movements in a test sequence as described in Fig. 1*A* left. Angular displacement record in *A* refers to top record of velocity only.

subjects, short periods could be identified which exhibited very distinct and regular 8–10 Hz cycles during the voluntary ramps. Individual subjects produced roughly similar profiles in successive sessions separated by several days or weeks, indicating that the inter-subject differences were genuine and not a result of temporary fluctuations.

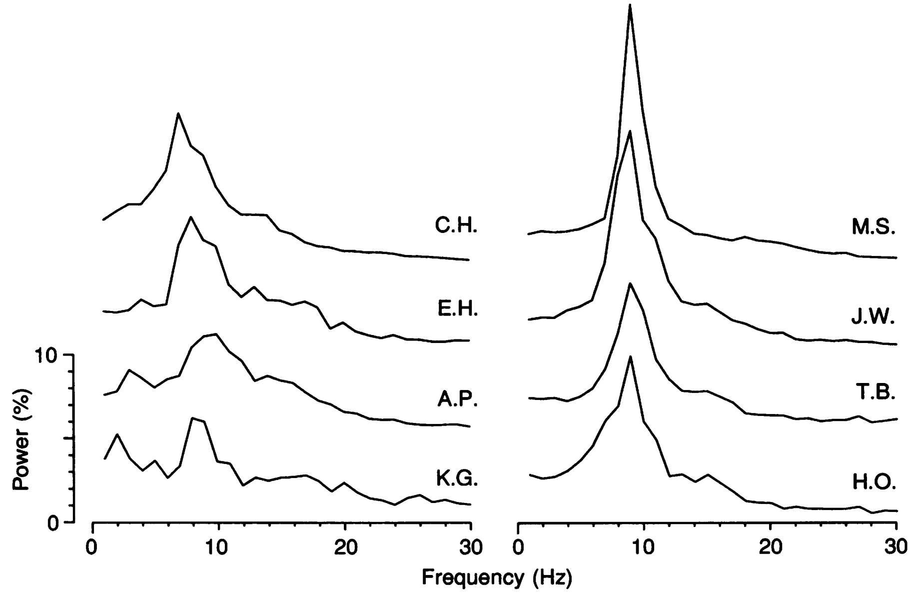

Fig. 3. Power spectra of acceleration records of eight subjects. The database consists of non-loaded extension movements with a track speed of 10 deg/s. Initials give subjects' name code. Individual spectra are averages of 42–204 movements. Curves are offset by a distance corresponding to five percentage points on the *y*-axis. Original recordings from subjects M.S. and A.P. are illustrated in Fig. 2.

Analysis of power spectra

A quantitative description of the frequency content of larger data sets was achieved by calculating the power spectra as described in Methods. Figure 3 displays power spectra from eight subjects, based on a fair number of movements performed under identical conditions (see legend).

The power spectra demonstrate a peak in the range 8–10 Hz for all subjects, although its height varied considerably between individuals. Additional peaks were seen at 2–3 Hz with two subjects (A.P., K.G.). Although not present in Fig. 3, peaks at higher frequencies were seen under different conditions, as will be described below.

The two subjects of Fig. 2 are represented as M.S. and A.P. in Fig. 3. The amount of 8–10 Hz discontinuities in their movements is also reflected in the power spectra of Fig. 3 which were based on a large number of trials. Incidentally, the qualitative relationship between characteristics of velocity profiles and power spectra may be intuitively appreciated from a comparison between Figs 2 and 3.

Ubiquity of 8–10 Hz discontinuities

The presence of the 8–10 Hz periodicity was not dependent on the particular features of the protocol trials (see Methods), but it was seen in a variety of conditions. The 8–10 Hz cycles were, for instance, present when the precision requirement was turned down by giving very loose instructions just to move the finger. It was seen also when the finger was not splinted, and when other fingers were used. Moreover, 8–10 Hz discontinuities were usually seen in the very first run after the subject had entered the laboratory as well as after a long experimental session. This latter finding suggests that novelty of task was not essential for the 8–10 Hz periodicity. This contrasts to the findings of Brooks (1974) on discontinuities with elbow movements in monkeys. Brooks emphasized that the monkeys 'tended to use discontinuous movements when the task situation had been changed or when they were unsure about what was expected'. It should be noticed, however, that the discontinuities studied by Brooks occurred at a lower frequency and may be of different nature altogether.

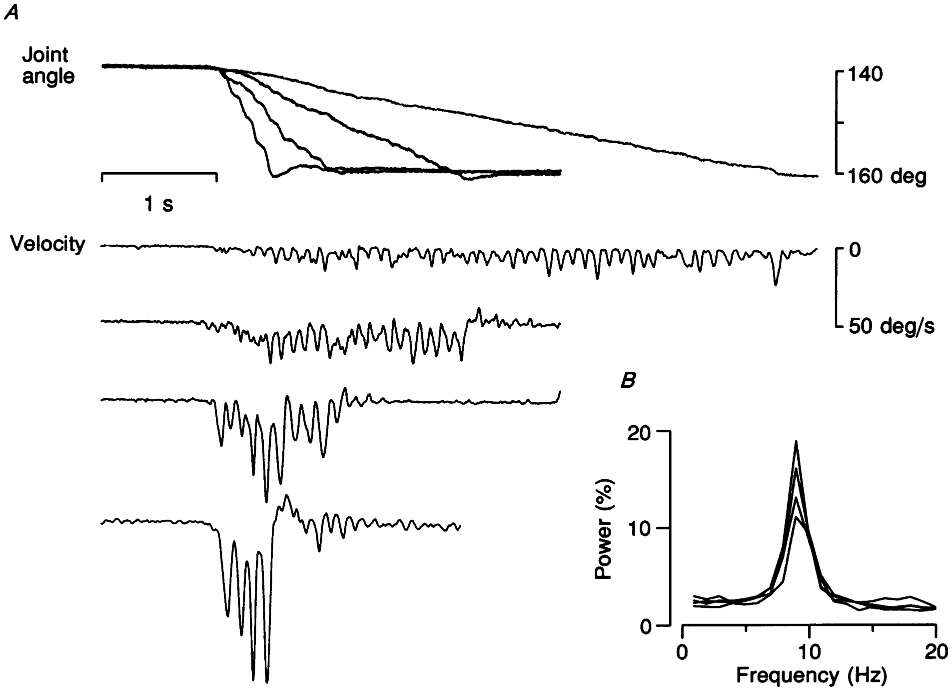

Fig. 4. Sample records to demonstrate subjects' performance in voluntary ramps of varying velocities. Upper records in *A* show angular displacement and lower records the corresponding angular velocities. The track speeds were 4, 10, 25, and 62 deg/s. *B* shows power spectra from 160 records of the same subject when tracking the same four track speeds. Data from subject M.S.

Contextual factors

Factors of relevance to the amount of 8–10 Hz discontinuities were explored in qualitative and quantitative analyses using the protocol of Fig. 1.

Velocity of movements

The 8–10 Hz discontinuities were not vitally dependent on the speed of voluntary ramps but they were present in movements whose overall velocity varied considerably as illustrated by the sample records of Fig. 4*A*. That frequency was independent of overall speed of the ramps is substantiated by Fig. 4*B* which shows power spectra for a larger set of data. On the other hand, it is obvious that the amplitude of the individual movement cycle was larger in fast movements. In Fig. 4 the amplitude clustered around 0·4 deg in the slowest movements (track speed 4 deg/s) to about 6 deg in the fastest movements (track speed 62 deg/s).

A similar dependence has previously been emphasized by Navas & Stark (1968) for a different type of discontinuity, i.e. 2·5 Hz saccades in wrist rotations when human subjects were tracking unpredictable targets under visual control. However, in addition, their report presents a few records from subjects tracking predictable ramps suggesting the same dependence for 8–10 Hz discontinuities, i.e. that step size increased with overall speed of the voluntary ramp.

Visual input

It has been emphasized that tracking of unpredictable targets under visual control is performed as a series of 2–3 Hz saccades (Navas & Stark, 1968). Although we studied responses to predictable targets, it was found that visual tracking occasionally promoted 2–3 Hz discontinuities. This was very evident in one subject as illustrated in Fig. 5 where *A* displays sample records with and without visual control. Power spectra based on a large number of movements demonstrated that the dependence of the 2–3 Hz discontinuities on visual feedback as seen in Fig. 5*A* was general in this subject (Fig. 5*B*).

On the other hand, the number of 2–3 Hz cycles as well as the effect of visual information was not consistent but varied considerably between subjects. Hence most subjects had far fewer 2–3 Hz cycles although the incidence was slightly higher when they were first confronted with the tracking task (not illustrated). Moreover, in most subjects visual information had no effect at all in this respect.

Flexion versus extension movements

The protocol trial included ramp-shaped movements, in the flexion as well as the extension direction, of the same overall speed and amplitude. A general finding was that the 8–10 Hz discontinuities were slightly more pronounced during extension movements than during flexion, as illustrated in Fig. 2. This difference was consistent as it emerged in power spectra of all subjects (not illustrated).

Motor skill and handedness

The 8–10 Hz discontinuities were present in subjects with varying motor skills and they were present in preferred hands as well as in non-preferred hands. In

Fig. 3 the power spectrum labelled M.S. originates from the preferred hand of a semi-professional cellist, i.e. a skilled and well trained hand, whereas the power spectrum labelled C.H. originates from the non-preferred hand of a subject who claimed poor manual skill, i.e. a non-skilled hand.

Effect of load and co-contraction

The 8–10 Hz discontinuities were not vitally dependent on a low degree of muscle activation, because they were present when the muscles worked against a range of

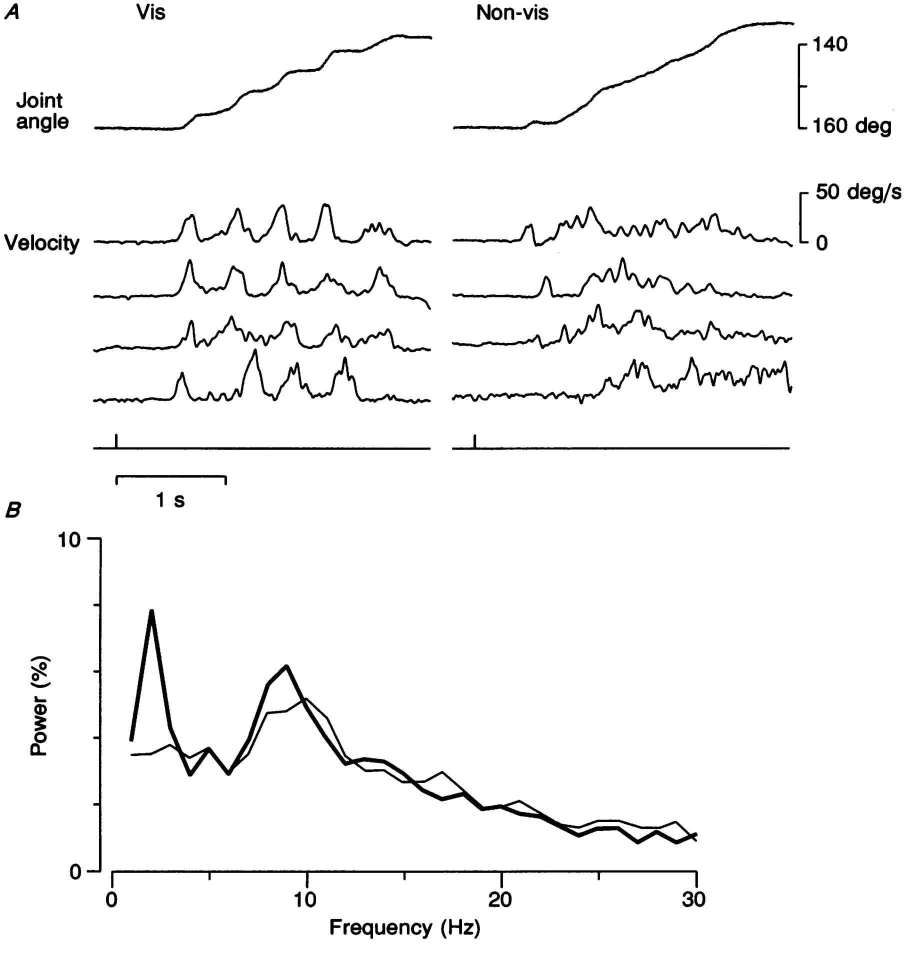

Fig. 5. Visual information promoted 2–3 Hz discontinuities. Performance of voluntary ramp movements with and without visual tracking. *A* shows performance in flexion ramps with a track speed of 10 deg/s; left, visual tracking; right, when subject was asked to reproduce from her memory an identical ramp (cf. Fig. 1). Angular displacement records refer to top records of velocity. *B* shows power spectra from the same subject, heavy line from visual feedback tracking and thin line without visual feedback. Spectra based on twenty-four flexion and twenty-four extension movements. Data from subject K.G.

constant-torque loads. On the other hand, addition of constant-torque loads had a clear effect on the overall kinematics. This was also true when the subject was instructed to tense his muscles by strong co-contraction during the voluntary ramp. These factors promoted discontinuities in the range above 20 Hz with peaks in the power spectra in the range 20–35 Hz (not illustrated). Since it has been shown that the natural frequency of the finger is in the frequency range above 20 Hz (Halliday & Redfearn, 1956; Stiles & Randall, 1967), it seems reasonable that these peaks, represent, at least partly, oscillations at the mechanical resonance of the finger.

Oscillations during position holding

Although the present study was focused on the kinematics of voluntary movements it should be pointed out that 8–10 Hz velocity variations were not definitely limited to the voluntary ramps but oscillations of similar rate and similar amplitude were occasionally seen between movements, i.e. during the phases of position holding. When they were present they were most prominent in the wake of the voluntary ramp movement, successively decreasing in amplitude.

It was found that co-contractions and large constant-torque loads promoted 8–10 Hz velocity variations during position holding and sometimes extended the duration to the entire hold phase. Moreover, they were more pronounced in the extended position than in the flexed position with our protocol trials.

It should be stressed, however, that in most runs, any tremor during hold phases was of a much lower amplitude than the 8–10 Hz discontinuities during voluntary ramps as illustrated in Figs 1, 2, 4, and 5.

Acceleration profile was asymmetrical

Analysis of the kinematics of the individual 8–10 Hz cycles during voluntary ramp movements revealed interesting features (Fig. 6).

The individual movement cycle started with an acceleration which was followed after some 30–50 ms by a prominent deceleration. As illustrated in Fig. 6, the acceleration peaks were usually smaller than the following deceleration peaks. This feature is also illustrated in Fig. 1*B* where it may be appreciated that most of the deceleration peaks during extension as well as during flexion are larger than the preceding acceleration peaks. This asymmetry was present in most 8–10 Hz cycles, regardless of track speed and direction of movement, although it was not absolutely consistent. The high deceleration peaks might be partly due to a recoil of energy stored in the series elastic elements of muscle and tendon during acceleration. Analysis of passive mechanisms indicated a small net force towards flexion over the major part of the angular working range under steady-state conditions when subjects were relaxed. Since the asymmetries with regard to peaks of acceleration and deceleration were not different in flexion and extension ramps, it seems unlikely that the asymmetry of passive forces was essential. The nature of the asymmetrical velocity profile was further elucidated by EMG recordings as will be described below, indicating that active mechanisms were involved.

A closer analysis of the kinematics of the individual 8–10 Hz movement cycles revealed yet another interesting feature. In very slow voluntary ramps, the velocity often lingered at zero for short intervals between phases of angular movement, as illustrated in Fig. 6*A*. Thus, the voluntary ramps were, at least partly, implemented as a series of displacements alternating with short intervals when the position was held stationary. In slightly faster ramps, a feature of probably similar nature was seen. Figure 6*B* illustrates that the fast deceleration was regularly followed by a phase of relatively moderate changes, often associated with a notch in the acceleration record, before the next phase of acceleration appears.

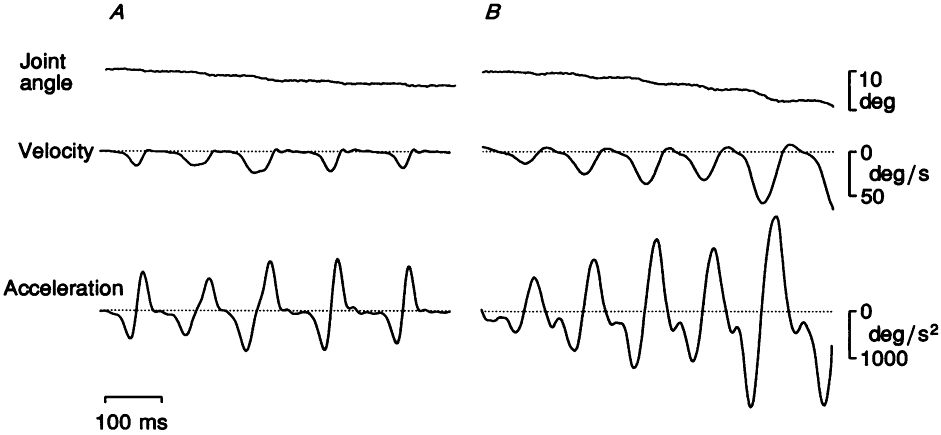

Fig. 6. Kinematics of individual movement cycles at slow ramp movements. Records show from above, angular displacement, angular velocity, and angular acceleration. Records from two different subjects T.B. (*A*) and A.P. (*B*). Note that the angular deceleration reached higher peak values than the preceding acceleration, as also illustrated in Fig. 1*B*. Three phases could be discerned in the individual cycle, i.e. acceleration, deceleration, and stand-still (left) or low velocity (right).

Hence, three consecutive phases may be discerned in the individual step or discontinuity of very slow voluntary movements. The first phase is one of acceleration and movement initiation. This is followed by a phase of deceleration which usually reached a higher peak level than the preceding acceleration. The third phase is characterized by relatively modest changes of velocity and position or none at all, i.e. a short period of stationarity. Obviously the individual movement cycles are highly non-sinusoidal.

EMG analysis indicated a complex agonist–antagonist interaction

The intricate kinematics of the individual movement cycle prompted a detailed analysis of the relationship between EMG activity of the working muscles, on the one hand, and the movement parameters, on the other. EMG activity was, in separate experiments, recorded either from the finger extensor muscle alone or from the finger flexor muscles as well. An emphasis on recordings from the former was justified since this muscle was the one and only extensor of the metacarpophalangeal joint whereas flexion can be accomplished by the superficial and deep finger flexors, as well as by the intrinsic interossei and lumbricals. In addition, the finger extensor muscle has a superficial location suitable for recording surface EMG. Figure 7 illustrates the relationship between the kinematics and the activity of this muscle.

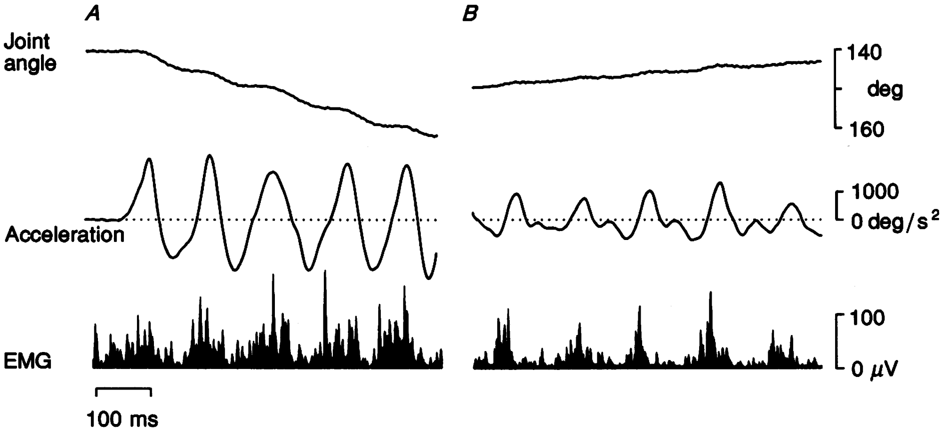

Fig. 7. Activity of finger extensor muscle was modulated in relation to accelerations of extension movements (*A*) and in relation to decelerations of flexion movements (*B*). Cross-correlation analysis indicated that modulations of the EMG activity preceded the modulations of the acceleration by 17·5–25 ms. Records from above, angular displacement, angular acceleration signal (inverted to match EMG record), and original root-mean-square-filtered EMG records. Track speed 25 deg/s in *A* and 10 deg/s in *B*. Data from subject M.S.

An obvious relationship was found between angular accelerations and modulations of the extensor EMG during voluntary extension ramps, as expected considering that this muscle was driving this movement. These modulations were seen in all sixteen subjects studied. A cross-correlation analysis of the sample records of Fig. 7*A* revealed a peak correlation coefficient of 0·47 at a time shift of 17·5 ms, EMG activity preceding acceleration. These findings suggested that the individual phase of acceleration was produced, at least partly, by a phasic modulation of the shortening muscle's activity, as the time shift at peak correlation corresponds to the electromechanical latency.

Modulations of the finger extensor EMG was, however, not limited to agonist movements. An obvious relationship was also found, during flexion movement, but now between the increases of EMG activity and the decelerations. Figure 7*B* illustrates this relationship. Cross-correlation analysis of the panel data indicated a lag of 25 ms at the peak correlation coefficient which was 0·69. Hence, the time shift was consistent with the EMG modulations contributing to the decelerations.

The amount of EMG activity picked up from the finger flexor muscles on the forearm was in general less prominent during these movements. However, a clear EMG activity was recorded in some subjects with free movements and could usually be provoked in others by loading the muscle or asking the subject to co-contract.

Similar modulations as in the extensor muscles could then be discerned. Sample records of a few cycles are shown in Fig. 8 which illustrates a segment of a free flexion movement. It may be appreciated that both the finger flexor and extensor muscles were modulated in close relationship to the kinematics in a pattern consistent with a biphasic motor output, i.e. a driving pulse to the agonist followed by a braking pulse to the antagonist.

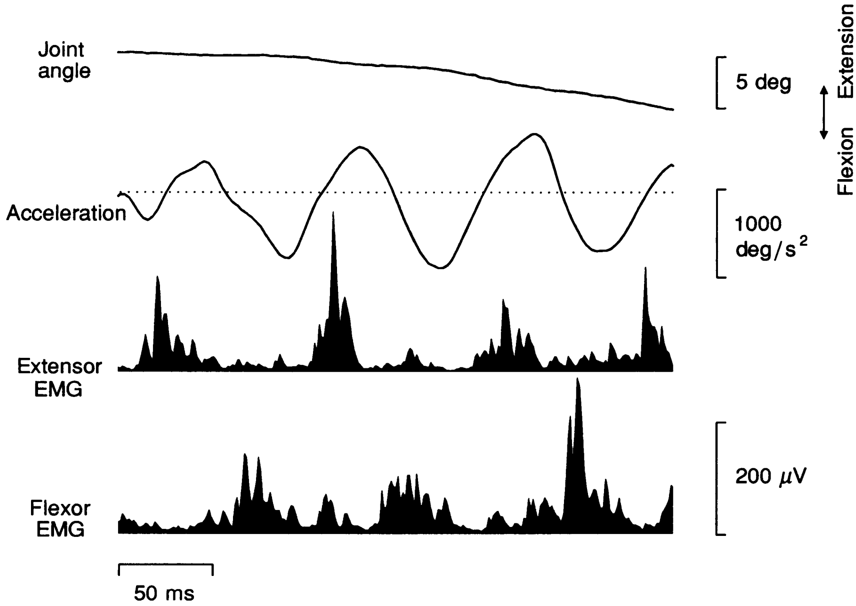

Fig. 8. Activity of both the finger flexor and extensor muscles was modulated in relation to kinematics. Records from above, angular displacement, angular acceleration signal, and original root-mean-square-filtered EMG records from forearm extensor and flexor muscles. Data from subject P.J. (not represented in Fig. 3).

DISCUSSION

It was shown that slow finger movements usually comprised a series of discontinuities or minute steps of movement recurring at a rate of eight to ten per second, each cycle comprising two phases, i.e. one phase of acceleration and high speed of angular movement, and one phase of deceleration. The repetition rate was uniform and independent of overall speed, whereas the angular amplitude of the individual step was larger the higher the speed. In very slow ramp movements, a third phase was discerned, i.e. the deceleration was often followed by a short period of stand still when the joint was kept immobile for some tens of milliseconds.

Discontinuities at 8–10 Hz during movements have previously been reported in a few studies (Marshall & Walsh, 1956; Young & Hagbarth, 1980) whereas a smooth profile has often been emphasized in movements of proximal joints (Soechting, 1984; Atkesson & Hollerbach, 1985; Fisk & Goodale, 1985). This may be related to the inertia of the moving parts. For finger joints where small masses are moved, a pulsatile motor output would more likely give saccade-like movements than for more proximal joints where the moving parts have larger inertias. On the other hand, it has been claimed that myoelectric activity tends to be modulated at a rate of 8–10 Hz in many different muscles (Lippold, Redfearn & Vuco, 1957).

Design of the motor output during ramp movements

It seems obvious that the 8–10 Hz discontinuities as described in the present report were accounted for by a periodic modulation of motor output from the central nervous system. This conclusion was supported by analyses of the myoelectric signals which indicated a relative synchronization of motoneuron activity in phase with the discontinuities. It was shown that modulations of the EMG activity of the agonist muscle preceded angular accelerations by a few tens of milliseconds, and similarly modulations of the antagonist preceded the angular decelerations by a similar amount. Mechanical resonance could be rejected altogether because 8–10 Hz is well below the natural frequency of the finger (about 25 Hz) (Halliday & Redfearn, 1956; Stiles & Randall, 1967; Marsden, 1984).

These findings suggest that the individual step during voluntary ramps was implemented by a biphasic motor output, i.e. an increase of motor unit activity in the shortening muscle propelling the movement, and, a few tens of milliseconds later, an increase of the activity in the antagonist exerting a braking action and curtailing the forward movement.

The biphasic pattern from the agonist and the antagonist was not seen under all conditions because our recording sometimes failed to pick up any EMG activity from the finger flexor muscles on the forearm. This may be due to a number of factors. First, the flexor muscles on the forearm are more remote from the skin surface and therefore the recording conditions are less favourable. Second, these muscles are much stronger than the extensor muscles and a smaller proportion of motor units would need to be activated for a given force. Third, the flexor muscles see a smaller load due to the low mass of extensor muscular tissue. Moreover, in the recording position of the hand, the passive forces tended to assist flexion movement which then would require less muscular activity. Finally, there remains the possibility that the flexing action was largely exerted by the intrinsic hand muscles which were not recorded in the present study.

Relation to tremor

It seems to be generally held that physiological finger tremor and enhanced physiological tremor in postural tasks, on the one hand, and discontinuities in the 8–10 Hz range during movements on the other, are of the same nature (Young & Hagbarth, 1980; Marsden, 1984). However, a number of differences between postural tremor and the present 8–10 Hz discontinuities indicate a need for some caution in equating the two altogether.

The size of the angular displacement of the constituent cycles may be vastly different. The 8–10 Hz discontinuities of the present study corresponded to displacements which amounted to 6 deg in faster movements whereas postural finger tremor seems to be more than an order of magnitude smaller (Halliday & Redfearn, 1956; Lippold, 1970; Hagbarth & Young, 1979; Young & Hagbarth, 1980; Marsden, 1984).

In postural tremor, the joint is periodically moving back and forth about a neutral position. During voluntary ramps, on the other hand, the motion is consistently unidirectional and the discontinuities simply imply periodic speed variations in the desired direction.

The tremor beat in enhanced physiological tremor seems to be roughly symmetrical whereas it was demonstrated in the present study that discontinuities during finger movements are often highly asymmetrical in two respects. One is that the peak deceleration is higher than the peak acceleration. It should be noticed that this asymmetry was evident with movements in both directions and therefore is probably not associated with the difference in mechanical conditions for flexion and extension movements. The other is that the 8–10 Hz discontinuities were often interspaced with short phases of stand still or very low speed in slow ramp movements. Since these features have not been described for tremor during position holding, they suggest a basic difference between physiological tremor and the speed modulations studied in the present investigation.

Reflex mechanisms

There seems to be good evidence that the 8–10 Hz oscillations in physiological position tremor are dependent on the stretch reflex although other mechanisms have been advanced as well, including a pulsatile supraspinal command (Lippold, 1970; Hagbarth & Young, 1979; Young & Hagbarth, 1980; Burne, Lippold & Pryor, 1984; Marsden, 1984; Sanes, 1985).

When considering the stretch reflex in relation to the discontinuities described in the present study, two points are particularly relevant. One is that the latency of the spinal stretch reflex is consistent with a role in generating 8–10 Hz modulations, whereas the long-latency stretch reflex favours a lower frequency (Stein & Oguztöreli, 1976; Marsden, 1978). Actually, the long-latency reflex tends to repress 8–10 Hz modulations of muscular activity. Second, the spinal stretch reflex is weak in many muscles during active movements particularly in comparison with the long-latency reflex (Melvill-Jones & Watt, 1971; Vallbo, 1974; Crago, Houk & Hasan, 1976; Marsden, Merton & Morton, 1976; Houk & Rymer, 1981). This was also confirmed for the type of movements studied in the present investigation (J. Wessberg & Å. B. Vallbo, unpublished observations).

Hence it seems unlikely that the stretch reflex is the major mechanism behind the 8–10 Hz discontinuities during voluntary movements, although it cannot be excluded that the spinal reflex may play a minor role.

A descending pulsatile output?

In the light of these arguments against the stretch reflex producing the discontinuities during movements it is important to consider the possibility that the central command for the voluntary finger movements as studied in the present investigation is basically pulsatile, rather than smoothly changing (cf. Navas & Stark, 1968; Brooks, 1974). This would imply that finger ramp movements are implemented by a central command pattern consisting of a series of short-lasting chunks of excitatory drive, i.e. one excitatory pulse to the agonist, followed by a short-lasting excitatory pulse to the antagonist.

An observation which seemed to support such an interpretation was the finding that very slow voluntary ramps often consisted of a series of saccade-like movements, separated by distinct, albeit short periods of standstill (Fig. 6). It is difficult to explain such steps as a result of oscillations in a reflex loop. Rather, a chain of movement steps is more easily conceived as the result of a series of excitatory pulses from central structures separated by periods of proper balance between agonist and antagonist muscle forces.

The idea that supraspinal motor commands for slow movements comprise a series of pulses recurring at a relatively regular rate seems attractive from several points of view. First it would suggest that higher motor centres are playing with two basic command patterns when controlling finger actions. One command pattern would implement position holding when the agonist and the antagonist muscle activities balance. Another central generator would produce the biphasic pulse pattern, characterized by an agonist burst preceding an antagonist burst by a few tens of milliseconds. A number of such biphasic command patterns would be concatenated at a rate of 8–10 Hz in order to implement slow finger movements, while a pulse height regulator may be postulated to set the overall speed of the voluntary movement. A clock device which may be involved in non-continuous control of motor output has been suggested to exist in the olivocerebellar system, providing intermittent co-ordination of premotor signals (Llinás, 1991). An additional element would be required in order to update the command pattern for position holding with regard to the new muscle lengths (Polit & Bizzi, 1979).

The idea of a biphasic pulse generator running repetitively to produce slow movements is appealing also from the point of view that the particular pattern of activation of agonist and antagonist, as seen in the present study, is reminiscent of the triphasic pulse strategy which has been amply demonstrated in fast movements as well as in production of force steps under isometric conditions (Wachholder & Altenburger, 1926; Hallet, Shahani & Young, 1975; Ghez & Gordon, 1987). The hypothesis would suggest that a similar command pattern, as utilized to implement fast movements and force steps, may constitute a basic building block of slow movements as well (cf. Brooks, 1974). In this context, it is of interest that the triphasic EMG pattern associated with fast movements has been suggested to be composed of two overlapping biphasic EMG pulses (Cooke & Brown, 1990).

This study was supported by the Swedish Medical Research Council (grant 14X-3548), Magn Bergvalls Stiftelse, and Knut och Alice Wallenbergs Stiftelse. We would like to thank Dr J. J. A. Scott for valuable comments on the manuscript.

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