Coding of pulsatile motor output by human muscle afferents during slow finger movements

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1. Impulse activities of thirty-eight muscle spindle and tendon organ afferents from the finger extensor muscles were recorded in the radial nerve of human subjects while the subjects performed voluntary flexion and extension finger movements at a single metacarpophalangeal joint.

2. The afferent firing was analysed in relation to the 8–10 Hz discontinuities which previously have been shown to characterize these movements. Spike-triggered averaging and frequency domain analyses demonstrated that all Ia muscle spindle afferents and a large proportion of group II spindle afferents responded in close association with local peaks in the joint acceleration. During muscle lengthening the impulses appeared during phases of rapid muscle stretch, whereas they appeared during the phase of minimal speed during muscle shortening.

3. The Golgi tendon organ (Ib) afferents displayed a reverse pattern of activity in relation to the discontinuities, i.e. the impulses tended to appear in the phase of minimal speed during lengthening movements and close to maximal shortening speed during shortening movements. Hence, their firing often coincided with the phasic increases of the parent muscle activity which account for the 8–10 Hz discontinuities.

4. A close analysis of the time relations between spindle firing and the kinematics of the 8–10 Hz discontinuities revealed that the population spindle response was too delayed and too dispersed to support the hypothesis that the discontinuities are accounted for by the stretch reflex.

5. If, as suggested in a previous paper, the 8–10 Hz discontinuities are produced by a pulsatile descending motor command, the coding of the periodic but tenuous kinematic events by the population of proprioceptors may have a role in relation to an alleged pulsatile command generator.

It has been demonstrated that slow finger movements are not smooth but are characterized by series of discontinuities, mostly recurring at intervals of 100–125 ms, corresponding to a frequency of 8–10 Hz (Vallbo & Wessberg, 1993). These small steps are brought about by modulations of muscular activity, either in the agonist alone when the antagonist is silent or in both muscles. The phenomenon is present over a wide range of movement velocities, the faster movements being implemented by a few discrete and relatively large steps.

Two sets of mechanisms may be involved in the production of 8–10 Hz discontinuities (Vallbo & Wessberg, 1993). The descending motor command might be pulsatile rather than smooth, or the discontinuities may be the result of modulation by spinal reflexes or other lower-level mechanisms. Both alternatives might have interesting implications. If the spinal stretch reflex accounts for the discontinuities, this reflex must be much stronger than generally assumed. If the descending motor command is pulsatile, it suggests that intermittency is a key feature of supraspinal control mechanisms (Llinás, 1991).

The role of muscle proprioceptors in relation to the 8–10 Hz pulses is altogether an open question although there are indications that muscle afferents may respond to minute speed variations. It is well established on the basis of animal experiments that muscle spindles may be extremely sensitive to small movements (Matthews & Stein, 1969; Hasan & Houk, 1975*a*, *b*; Cussons, Hulliger & Matthews, 1977; Hulliger, Matthews & Noth, 1977). Moreover, it has been pointed out that human spindle afferents often respond to small irregularities during voluntary movements, although systematic analyses of firing in relation to the kinematics are lacking (Vallbo, 1973, 1985; Burke, Hagbarth & Löfstedt, 1978).

In order to assess to what extent muscle spindle and Golgi tendon organ afferents code the 8–10 Hz discontinuities during voluntary finger movements, we have studied the activity of single afferents using the microneurographic technique. It was found that the firing of muscle primary and secondary afferents as well as tendon organ afferents is often modulated in relation to the 8–10 Hz discontinuities. It was concluded that the population response provides a marker of the occurrence of the discontinuity of individual movement. On the other hand, the temporal pattern failed to support a reflex origin of the 8–10 Hz discontinuities.

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

METHODS

Experiments were performed on fourteen healthy volunteers, seven females and seven males, aged 21–31 years. Informed consent 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 Göteborg University.

General procedure and equipment

The subject was seated comfortably 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 lightly flexed at a joint angle of 165–175 deg.

The activity of single unit afferents of the left radial nerve was recorded using the microneurographic technique (Vallbo, Hagbarth, Torebjörk & Wallin, 1979). The recording needle was inserted 5–7 cm proximal to the elbow. The search procedure consisted of repeated passive flexion–extension movements of the fingers, and localized poking over the finger extensor muscles (m. digitorum communis and m. extensor indicis proprius). Only units which responded with a sustained discharge to poking on the muscle belly or to passive flexion and/or voluntary contraction of the parent muscle were considered for further analysis.

The finger which elicited the best response from the unit was strapped to a splint which prevented movements at the interphalangeal joints but permitted metacarpophalangeal joint movements. The splint was attached to an actuator device by means of a low-mass hinged bar. The actuator has been described previously (Al-Falahe & Vallbo, 1988). Transducers of the actuator provided continuous recordings of metacarpophalangeal joint angle, velocity and torque. An integral servo-motor compensated for friction and inertia; thus the actuator device presented zero load to the moving finger. An oscilloscope in front of the subject was used for visual tracking. The beam was swept vertically and split into two halves, the top half displaying the desired target and the bottom half the actual joint angle. A microcomputer was programmed to control the actuator, the tracking oscilloscope and other equipment including a separate sampling computer.

EMG was recorded with surface electrodes placed on the dorsal surface of the forearm, over the area for minimum thresholds for transcutaneous electrical stimulation of the common finger extensor (Edin & Vallbo, 1987). The EMG was root-mean-square rectified with rise and decay time constants of 1·6 and 4·8 ms, respectively, and then sampled at 800 Hz on-line. The kinematic parameters were sampled at 400 Hz and the nerve signal at 12·8 kHz. Acceleration was derived off-line by low-pass filtering (−3 dB at 50 Hz and zero gain at 100 Hz) and differentiation of the velocity signal. Each recorded nerve spike was inspected off-line on an expanded time scale, and this validated nerve signal was used for subsequent unit classification and data analysis.

Unit classification

The recorded afferents were classified on the basis of eight criteria using a Bayesian evaluation procedure as described by Edin & Vallbo (1987, 1988, 1990*a*, *b*, *c*), i.e. each unit was subjected to ramp stretches; small sinusoidal oscillations superimposed on a ramp stretch; a test of intrafusal myofilament bonds; voluntary contractions ending with brisk relaxations of the parent muscle and maximal twitch contractions evoked by electrical stimulation.

Of the thirty-eight recorded afferents, twenty-three were found to be Ia, eight group II and seven Ib Golgi tendon organ afferents. Median probability values provided by the Bayes procedure were 0·99, 0·96 and 1·00 for the Ia, II and Ib units, respectively.

Experimental protocol

The main experimental protocol comprised a visual tracking task, each trial consisting of five phases: a position-holding phase; an extension movement of 20 deg; an intermovement position-holding phase; a flexion movement back to the initial position; and finally a position-holding phase. Auditory cues prompted the subjects to start the movement phases. The target moved with a constant speed corresponding to 10 deg s^{-1}, starting 0·3 s after the auditory cue. Subjects were given a training session of ten to twenty movement sequences, until they were adequately familiar with the procedure.

Slightly modified protocols were used in some experiments. In five experiments, the subjects performed additional non-visually guided movements in alternation with the visual trials, and were requested to mimic exactly the preceding visual tracking movement. In another three experiments, only extension movements were used, hence the unit database for extension movements is slightly larger than for flexion movements.

Altogether 820 movements were analysed, the number per unit ranging from seven to seventy-two.

Data analysis

Analysis was limited to phases of movement; the hold phases were ignored. Mean firing rates of the individual afferents during flexion and extension movements were calculated separately on the basis of data from all movements.

A series of statistical methods were employed to assess the relationship between afferent firing, on the one hand, and movement parameters and EMG, on the other. The temporal relation of unit activity *versus* other parameters was assessed using spike-triggered averaging. Corresponding analyses of the temporal relation between signals other than nerve activity were done by computing the cross-correlation (Bendat & Piersol, 1986).

To appraise the temporal variability of unit firing in relation to the phases of the individual discontinuity, histograms were constructed of the distribution of nerve impulses around the

acceleration peaks. Data for this analysis were selected on the basis of uniformity of the movement discontinuity with regard to size and shape. The procedure was, first, to pick out by eye at least thirty local acceleration peaks of fairly uniform shape and size. An average of these peaks was computed. All local peaks in the sample were then amplitude normalized. Their shapes were compared with the constructed 'reference' peak. A cycle was provisionally accepted if the root-mean-square difference did not exceed a specified value. It was finally accepted if the original amplitude of the acceleration peak was close to that of the reference. The proportion of cycles accepted was small because of the large variability in shape and amplitude. Hence, enough data for the construction of a histogram was obtained in a few units only.

For frequency domain analyses the trains of nerve impulses were treated as a point process, i.e. only the times of occurrence of the impulses were considered. Analog signals representing velocity, acceleration and EMG were handled as continuous processes with continuously changing values over time. Autospectra were computed by averaging the Fourier transforms of successive 1·28 s segments using the standard procedure appropriate for point processes (Bartlett, 1963; Amjad, Breeze, Conway, Halliday & Rosenberg, 1989) and continuous processes (Bendat & Piersol, 1986), giving a frequency resolution of approximately 0·78 Hz. Cross-spectra between two processes were then calculated and normalized as the coherence spectrum, which is a function describing the linear correlation squared between the two signals at a given frequency on a scale from zero to one. The statistical analysis of these spectra was done according to Bendat & Piersol (1986), Carter (1987), and Rosenberg, Amjad, Breeze, Brillinger & Halliday (1989).

All calculations were made on MS-DOS compatible PC-type computers, using software written in Borland Pascal by J. Wessberg.

RESULTS

The main purpose of the present study was to analyse the firing of muscle spindle and Golgi tendon organ afferents in relation to the 8–10 Hz discontinuities which are a prominent feature of slow finger movements. The test procedure comprised voluntary precision movements at a single metacarpophalangeal joint in both flexion and extension directions.

Muscle spindle afferents

The firing rates of spindle afferents were generally lower during extension than during flexion movements. For Ia units, the median rate was 11·3 Hz (range, 4·8–26·2 Hz) during lengthening and 4·2 Hz (range, 0–20·6 Hz) during shortening. Similar rates were found for group II

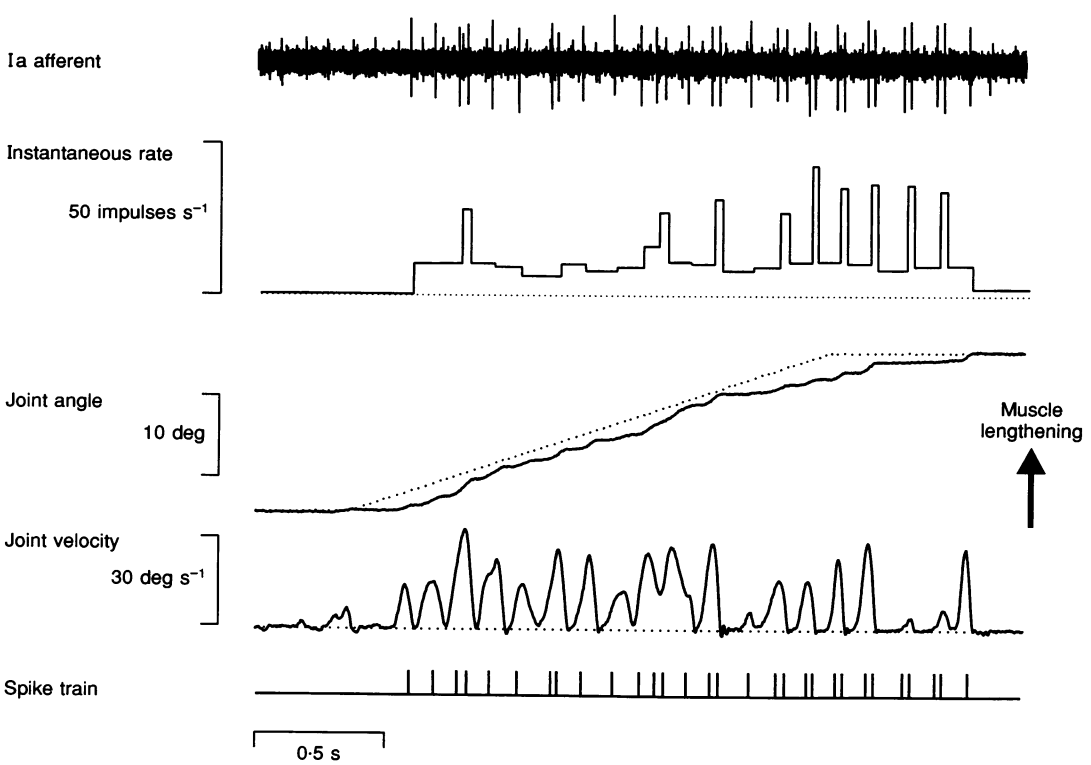

Figure 1. Microneurographic recording of a single muscle spindle Ia afferent during a voluntary finger flexion movement

Records from above: original nerve signal; instantaneous nerve impulse rate histogram; subject's performance and tracking signal (dotted line); velocity and a symbolic representation of the spike train. Note the strong component of 8–10 Hz discontinuities in this movement, and the strong correlation between unit firing and the individual discontinuities.

afferents, i.e. 10·2 Hz (range, 3·0–16·1 Hz) for flexion and 6·2 Hz (range, 0·2–13·5 Hz) for extension.

The higher rates during lengthening movements are consistent with the view that spindle firing is highly dependent on movement parameters and may code the direction of movement in this situation (Prochazka, Stephens & Wand, 1979; Hulliger, Nordh & Vallbo, 1985). More pertinent for the present issue, however, is that in many tests the afferent impulse rates were lower than the frequency of discontinuities.

A sample flexion movement is shown in Fig. 1. It is obvious that the trajectory contains a strong component of 8–10 Hz discontinuities, particularly evident in the velocity record. All subjects displayed this phenomenon, although to a varying degree, as described previously in detail (Vallbo & Wessberg, 1993).

Simple inspection of the records indicated that many spindle afferents had a tendency to fire in close relation to the 8–10 Hz discontinuities during lengthening as well as shortening movements. An example is shown in Fig. 1 with a primary afferent during lengthening movement. In the two bottom records it can be seen that impulses occurred mainly in the phases of the kinematic cycles when the velocity was high. More precisely, impulses tended to appear in close vicinity to the peak acceleration or peak velocity, as illustrated on a more expanded time scale with another unit in Fig. 2*A*. The response during the individual cycle usually consisted of a single spike, but sometimes double-spike (as in Fig. 1) or even triple-spike firing was seen.

During extension movements, when the parent muscle was shortening, spindle afferents exhibited a prominent tendency to fire in the phase when the angular speed was low or minimal which, in turn, was shortly after peak deceleration. This is illustrated in Fig. 2*B*. It should be emphasized that instantaneous angular speed seldom passed beyond zero during shortening movements. Hence spindle firing could not be a response to overt stretch of the muscle except in a small minority of cycles.

To obtain quantitative estimates of the temporal relationship between unit activity, on the one hand, and velocity, acceleration, and EMG, on the other, spike-triggered averages were constructed for all units. Figure 3 shows such averages of acceleration for four representative Ia and four group II afferents extracted from flexion movements. It can be seen that all the

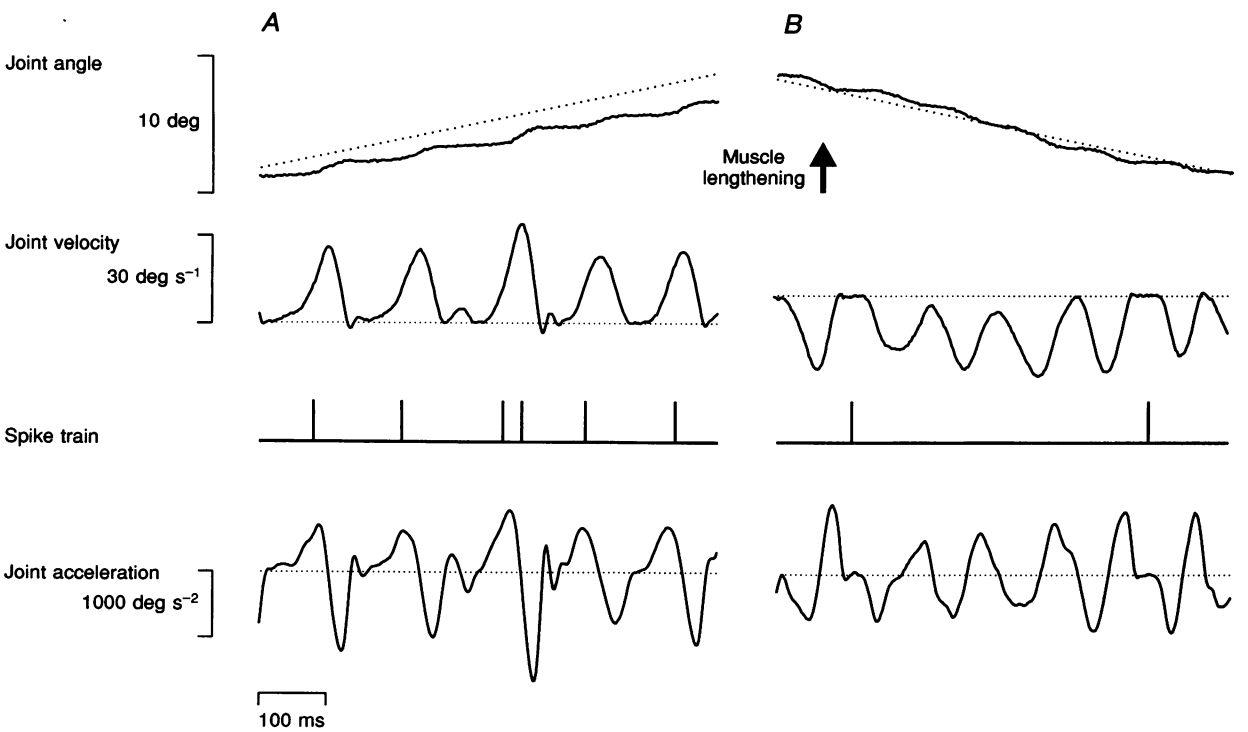

Figure 2. Details of Ia afferent recordings during voluntary finger movements

A, a detail of a finger flexion movement as in Fig. 1 shown on an expanded time scale. Records from above: joint angle and tracking signal (dotted line); velocity; a symbolic representation of the Ia afferent spike train and joint acceleration. The Ia discharges tend to occur close to the acceleration peaks. *B*, a corresponding detail from an extension movement, with data from the same unit. Note the conventions used for the direction and the sign of the velocity and acceleration; an acceleration in the positive sense now signifies deceleration of the movement. The overall discharge level is lower than in *A*, and the few spikes occur when the velocity approaches zero, after a preceding deceleration peak.

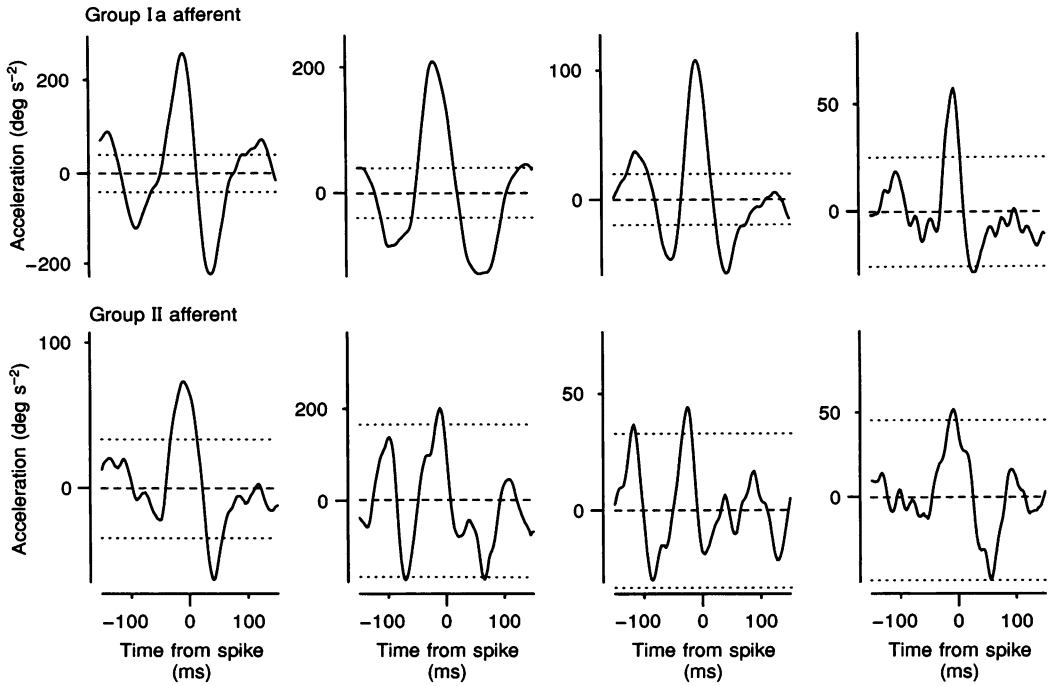

Figure 3. Spike-triggered averages of the flexion movement acceleration records

Top, 4 Ia afferents; bottom, 4 group II afferents. Dashed lines indicate the signal means and dotted lines the 99% confidence limits. The number of spikes per average range from 120 to 1154.

averages display a significant ($P < 0{\cdot}01$) peak of acceleration close to the unit discharge. Also note that there are peaks of lower amplitude 100–125 ms before and after the main peak, consistent with the units being modulated by the 8–10 Hz oscillations in the acceleration signal.

Considering the total sample, a significant peak was seen in 86% (18/21) of the Ia units and 50% (4/8) of the group II afferents (at $P < 0{\cdot}01$) for flexion movements. For the extension movements, the corresponding figures were 56 (13/23) and 25% (2/8), respectively.

The response to imposed sinusoidal stretchings was also explored while subjects remained relaxed as part of the identification procedure as described in Methods. When 50 Hz sinusoids with an amplitude of less than 1 deg (0·12 mm tendon excursion) peak-to-peak were applied in combination with ramp stretch (Edin & Vallbo, 1990*c*) all the units which we classified as

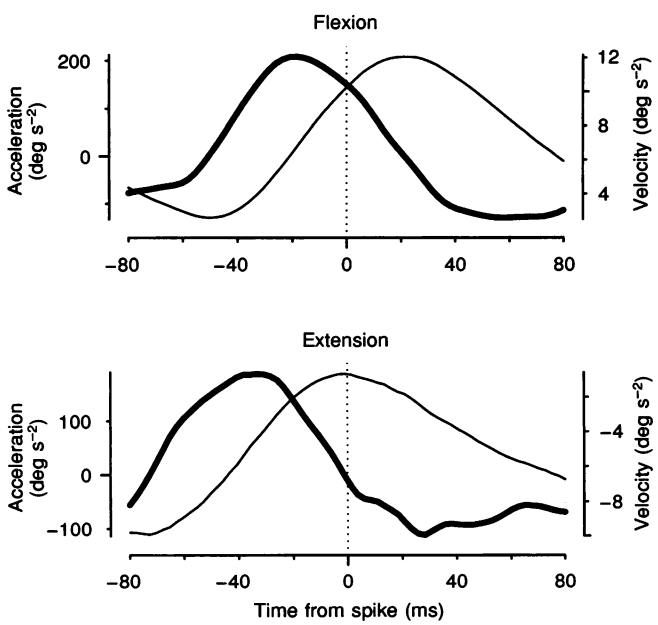

Figure 4. A comparison between spike-triggered averages of the velocity and acceleration records

Spike-triggered averages of velocity (thin lines) and acceleration (thick lines) records in flexion (top) and extension (bottom) movements for a representative Ia afferent. Note that unit activity on average is more delayed with respect to the kinematic events during extension.

primaries exhibited one-to-one driving during part of the stimulation period. In the units classified as group II, subharmonic driving was seen in 62% (5/8), and one-to-one driving in one unit.

In addition to the difference between flexion and extension with regard to mean impulse rate as described above, the time relation between spindle firing and kinematics of the individual discontinuity was also dissimilar in the two directions of movement. Figure 4 was constructed to illustrate this for a representative Ia unit. It can be appreciated that, for voluntary flexion movements (parent muscle lengthening), the impulse tended to occur roughly midway between peak acceleration and peak velocity. For extension movements, the firing was more delayed in relation to the kinematic events, i.e. the impulse tended to occur close to the peak of the velocity. Note that peak velocity during extension movements represents the minimal negative velocity, i.e. the point where the velocity approached zero during the kinematic cycle.

The temporal distribution of the peaks in the spike-triggered averages of acceleration for the whole database is summarized in Fig. 5. Note that the time scale is reversed in this diagram in relation to the average plots of Fig. 3, so that a positive time lag corresponds to a mean delay *from* peak acceleration *to* unit discharge. For the Ia units, the mean time lag for flexion movements was 9·0 ms (range, −17·5 to 20 ms) and for extension movements 23·7 ms (range, 7·5–37·5 ms).

Significance of conduction time

The question may be raised as to what extent the conduction times from the end organs to the recording site contributed to the variation of lags as shown in Fig. 5. In the total sample, the distances from the spindle, defined as the point on the forearm where the unit could be activated with local pressure, to the recording electrode were 7–25 cm. Considering a Ia conduction velocity in the range 60–100 m s^{-1}, this would give very short delays in relation to the interunit variations presented in Fig. 5, i.e. 1·2–4·2 ms. Furthermore, no correlation was found between the distance from the spindle to the recording electrode and mean lag. Hence conduction time cannot be a major factor in explaining the time variation between impulse and acceleration peak. However, to be strict, about 3 ms should be subtracted from the lags in Ia afferents given in the preceding paragraph to obtain the average time at which the spike is initiated in the spindles.

Spike-triggered averaging of EMG demonstrated a broad decrease in parent muscle activity preceding unit discharge by up to 50 ms with many units. This is illustrated for flexion movements in Fig. 6*A*. This finding is consistent with the interpretation that spindle firing was triggered by mechanical events in the muscle.

In one Ia unit alone, the EMG average displayed a sharp *positive* peak very close to zero lag time for both movement directions (Fig. 6*B*). This indicates a totally different causal relation between muscle activity and unit firing than in the other thirty spindle afferents. It suggests that the spindle impulse was triggered by the activity of a single motor unit. Whether this triggering was accounted for by β-innervation, a close α–γ linkage, or a mechanical effect of extrafusal contraction cannot be determined. The risk that the unit was a misclassified Golgi tendon organ afferent (see below) was ruled out because all identification tests indicated muscle spindle origin.

Additionally, cross-correlation analyses between EMG and acceleration revealed a close connection in all subjects, with EMG preceding negative acceleration (muscle shortening) by a mean value of 18·6 ms (99% confidence interval, 17·3–19·8 ms), representing

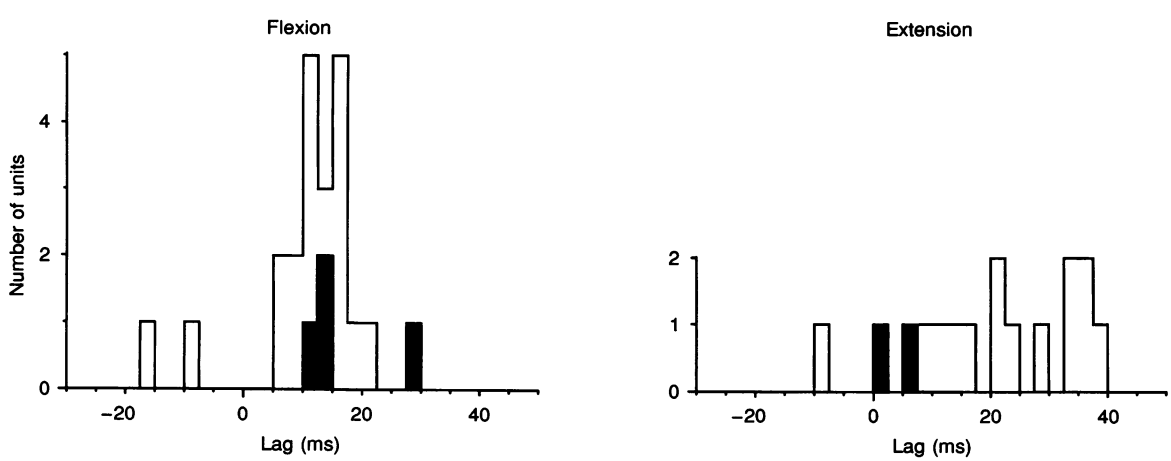

Figure 5. Distribution of mean acceleration to discharge lags for the population of muscle spindle afferents

Histograms of the distribution of time lags *from* peak acceleration *to* mean unit discharge for flexion (left) and extension (right) movements for all Ia (□) and group II (■) afferents where significant ($P < 0·01$) peaks existed in the spike-triggered averages.

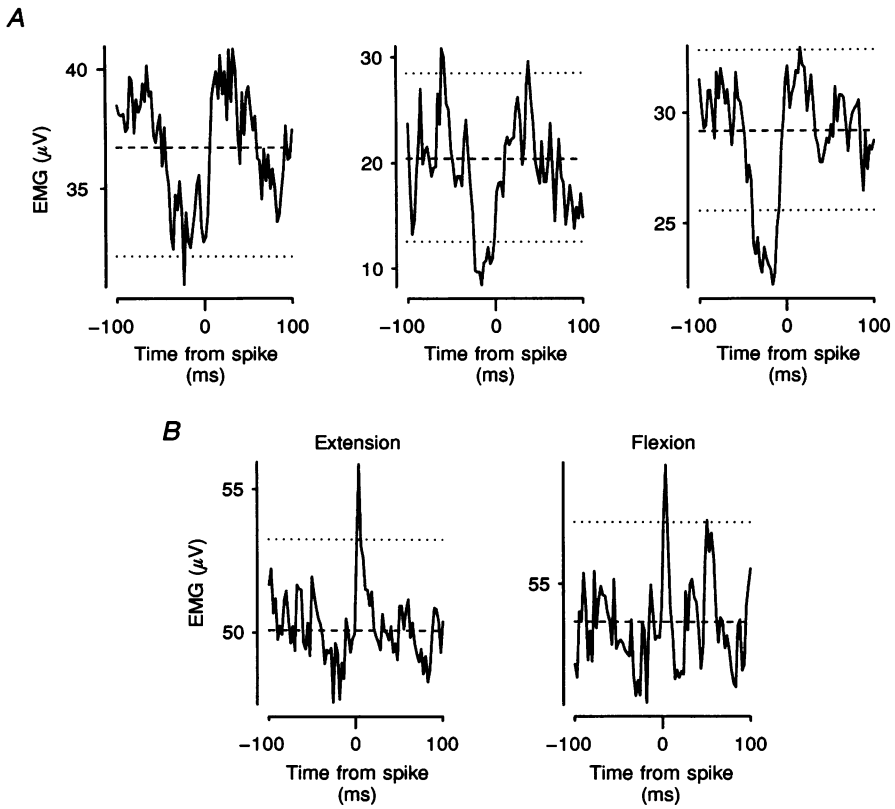

Figure 6. Spike-triggered averages of EMG records

A, spike-triggered averages of the flexion movement extensor EMG records for 3 Ia afferents. Dashed lines indicate the means, and dotted lines the approximate 95% confidence limits. *B*, spike-triggered average of EMG during extension (left) and flexion (right) for a unit that exhibited a sharp positive peak close to zero lag time.

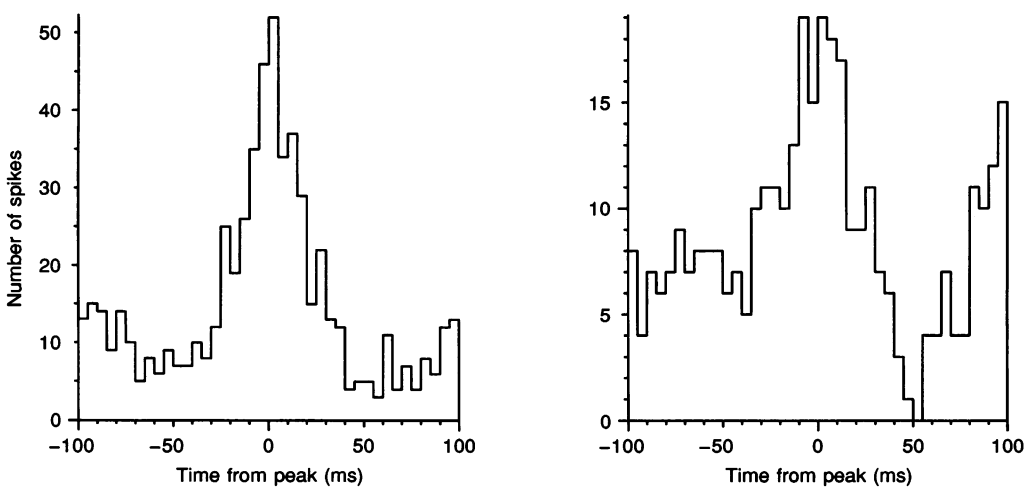

Figure 7. Long-term distribution of unit discharges around local acceleration peaks

Histograms of the distribution of unit discharges around acceleration peaks of similar amplitude and shape. Data are from flexion movements for 2 different Ia afferents. Only local peaks with a root-mean-square difference (after normalization of the peak to unity) from the reference of less than 5% and with a peak amplitude in the 400–1000 deg s^{-2} range were used. (See Methods.)

electromechanical delay. These figures are based on pooled data from extension and flexion movements since there was no difference between them.

Temporal variability within single-unit firing

The histograms of Fig. 5 provide estimates of the variability in the occurrence of unit discharges with respect to the kinematic events *for the whole population* of muscle afferents. In order to further analyse the temporal variability *for individual units*, histograms were constructed of the distribution of unit discharges with respect to local acceleration peaks of uniform amplitude and shape, according to the procedure described in Methods. Such histograms from two Ia units are shown in Fig. 7. The broad peaks imply that the discharges of individual units were not phase locked to the acceleration, but there was a considerable scatter around the peak acceleration. It can be appreciated that the temporal scatter of firing of the individual units was of the same order of magnitude, or even larger than, the variance in the population data of Fig. 5, as evident from the broad peaks of the histograms of Fig. 7.

Coherence spectra

A complementary analysis of unit activity in relation to acceleration in the frequency domain was done by computing auto- and cross-spectra as described in Methods. Figure 8 shows autospectra for acceleration and for firing of three Ia units sampled from the same movements, as well as the coherence between the two variables.

Significant coherence was often found in a broad frequency range below 12 Hz. Of particular interest in the present context is the 8–10 Hz range. It was found that, during flexion movements, as many as 67% (14/21) of the Ia units showed significant ($P < 0{\cdot}01$) coherence in this frequency range, mostly reaching peaks between 0·15 and 0·3 Hz (Fig. 8, lower right panel) although values amounting to 0·6 Hz was seen with 4 units (Fig. 8, lower left and middle panels). Moreover, the highest value of the coherence spectrum was often located in the 8–10 Hz band.

As would be expected from the time domain analysis, extension movements were associated with lower coherence values. Significant levels were attained in only 22% (5/23) of the Ia afferents. For the group II afferents,

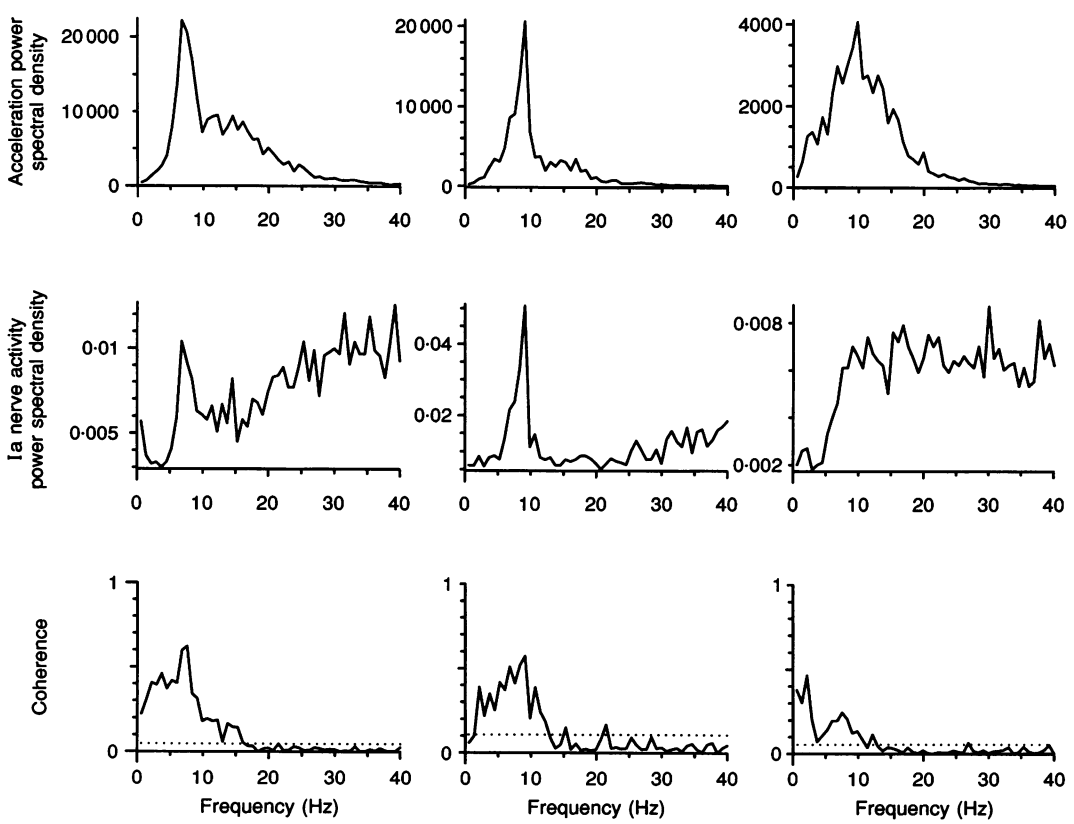

Figure 8. Frequency domain analysis for muscle spindle Ia afferents

Results for 3 different Ia units are shown. From above: power spectra of the acceleration, power spectra of the Ia unit discharge trains and coherence spectra between acceleration and nerve discharge. Note the 8–10 Hz peaks in these spectra. Dotted lines indicate the 99% confidence limit of the coherence.

2/8 showed significant coherence at 8–10 Hz during flexion movements, and none during extension.

A significant coherence at 8–10 Hz provides quantitative support for the interpretation that these units are modulated by the movement discontinuities at these frequencies.

Golgi tendon organ units

Units identified as Ib exhibited in many respects a reverse pattern compared with the majority of the muscle spindle afferents. Spike-triggered averages of the acceleration showed a *negative* peak close to unit discharge as illustrated for extension movements in Fig. 9. This pattern was seen in 67% (4/6) of the units during flexion, and in 57% (4/7) during extension ($P < 0{\cdot}05$). Using the same convention as in Fig. 5, the mean delay from the negative acceleration peaks to unit discharge was −7·5 ms in both flexion and extension (range, −27·5 to 5·0 ms), i.e. on average the tendon organ firing preceded the acceleration peak by 7·5 ms.

In considering the time relations between EMG, kinematics and Golgi tendon organ firing, it should be noticed that the parent muscle is particularly active during the phases when the acceleration is negative as defined in Fig. 9. This is true for extension movements when the parent muscle is actively shortening and hence driving the movement as well as for flexion movements when this muscle may contribute to the discontinuity by a braking action. In three out of seven tendon organs a distinct peak in EMG was found close to the occurrence of the impulse in spike-triggered averages (Fig. 9*B*).

The activity of these Ib units are in line with the well-established view that Golgi tendon organs are preferentially activated by contraction of the muscle inserting in the receptor-bearing tendon (Jansen & Rudjord, 1964; Houk & Hennemann, 1967; Jami, 1992). This is also compatible with findings in the cat emphasizing that Golgi tendon organs are particularly responsive to dynamic changes of the force output of the active muscle (Horcholle-Bossavit, Jami, Petit, Vejsada & Zytnicki, 1990).

DISCUSSION

Coding of 8–10 Hz discontinuities by muscle afferents

The present study demonstrates that a large proportion of group Ia and II muscle spindle afferents as well as Golgi tendon organ afferents are modulated in relation to the 8–10 Hz discontinuities described recently in slow finger movements (Vallbo & Wessberg, 1993). In many primary afferents the modulation was evident upon mere

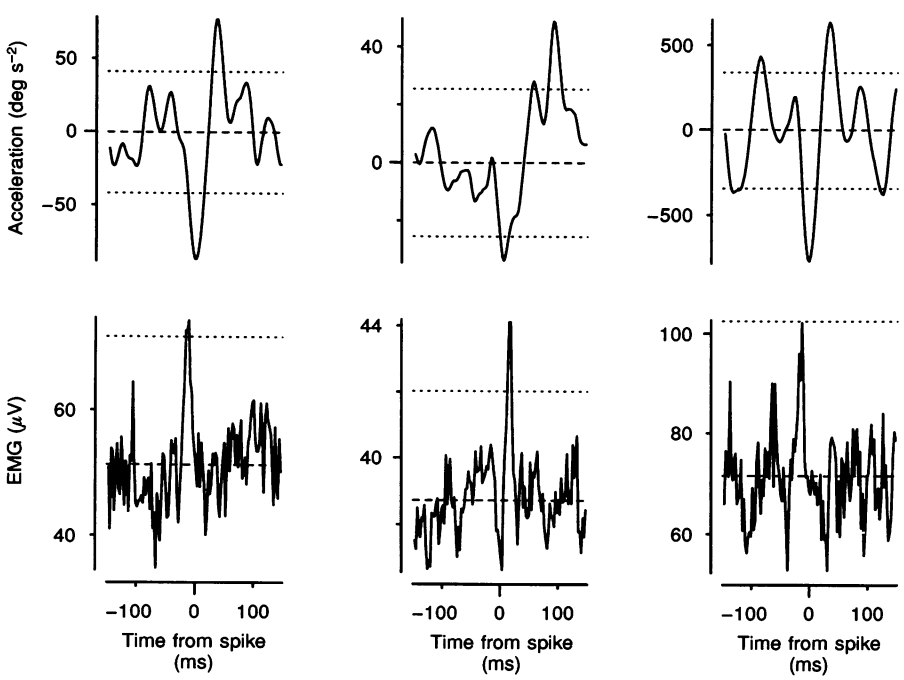

Figure 9. Spike-triggered averages for Golgi tendon organ units

Results for 3 Ib (Golgi tendon organ) units are shown. Top panels show averages of the extension movement acceleration records, and bottom panels the corresponding averages of the extensor muscle EMG records for the same 3 units and movements. Dashed lines indicate the signal means and dotted lines the 99% confidence intervals. The number of spikes per average range from 38 to 960.

inspection of raw data. Moreover, quantitative analyses in the time and frequency domains demonstrated significant correlations in additional primaries and also in a fair proportion of the units classified as secondaries. Altogether, the 8–10 Hz discontinuities were coded by about 90% of the muscle spindle primary endings and by 50% of the secondary endings. The coding of the discontinuities by the population of secondaries might be surprising considering the general view that they have a poor dynamic sensitivity. However, there is ample evidence from animal experiments that, in fact, many secondary muscle afferents may be quite sensitive to the dynamic aspects of movements (Matthews & Stein, 1969; Houk, Rymer & Crago, 1981).

Modulations of spindle firing in relation to the 8–10 Hz discontinuities were present during lengthening as well as shortening movements. In the former, impulses clustered in the phase of acceleration. With shortening movements, impulses appeared preferentially when the speed of shortening was at a minimum during the cycle. Hence in both lengthening and shortening movements, spindles tended to fire in the kinematic phase, which is most favourable for exciting a stretch receptor, although the triggering mechanisms should be different. During lengthening the phase of relatively rapid stretch promoted firing, whereas during shortening the phase of relatively slow movement allowed the fusimotor effect to launch impulses. The pattern of activity during shortening was thus interpreted as the result of a balance between fusimotor drive, on the one hand, which tended to keep the afferent firing up, and on the other, the kinematic effect, which tended to silence the afferent during the phase of relatively high speed of shortening. In the phase of the 8–10 Hz cycle when the spindle afferent fired, the parent muscle activity was decreasing. This was true for shortening as well as lengthening movements provided that the muscle was at all active in the latter.

These findings indicate that the time of occurrence of impulses was to a great extent determined by the kinematics of the movement and not by fusimotor effects. This is not to deny, however, that fusimotor activity might have had a strong influence on other features of spindle firing during these movements.

The majority of the tendon organ afferents exhibited a reversed pattern and fired in the opposite kinematic phase compared to the muscle spindle afferents, i.e. the phase when the parent muscle was particularly active. Moreover, in some Ib afferents, it was demonstrated that impulse firing was associated with a distinct increase in EMG, probably accounted for by the activity of the motor units inserting on the sense organ.

The majority of the muscle spindle afferents can thus be considered detectors of the 8–10 Hz discontinuities. Another issue is whether, in addition, the response contains quantitative information on the size and shape of the individual discontinuity. It may be speculated that such information would be useful for the precision control of the on-going movement, beyond the level of simple reflex effects. Since coherence is essentially the linear correlation squared between two variables at a given frequency, the significant coherence at 8–10 Hz, which was present in 67% of the Ia units, would indicate that on average higher acceleration peaks give larger responses. However, it should be noted that all movements in the present study were performed at the same overall movement velocity. As a consequence the kinematics and the discontinuities were fairly uniform. It would be of great interest to analyse spindle responses to larger steps which develop with faster finger movements (Vallbo & Wessberg, 1993) in order to explore to what extent the population response increases *pari passu* with step size.

Since both muscle spindles and Golgi tendon organ afferents respond to the 8–10 Hz discontinuities, the central nervous system would have access to two separate afferent channels coding the 8–10 Hz discontinuities. Our findings indicate that there was roughly a 180 deg phase shift between the population response of spindles and tendon organs with regard to the 8–10 Hz step cycle implying that they were coding the decelerative and accelerative phases of these cycles separately. Hence central motor structures are offered the option of extracting separate information on the acceleration and deceleration pulses. This information might be useful not only to verify the peripheral events but also to tune the central mechanism which produces the agonist and antagonist muscle pulses accounting for the discontinuities, so that these pulses are appropriately balanced in order to assemble the desired movement.

Due to the lower overall activity of the muscle spindles in the shortening agonist, the central motor structures would have to rely largely on afferent information from the lengthening antagonist. This is in line with reports showing that sensory input from the antagonist appears to be particularly important for the continuous regulation of wrist and elbow movements (Cussons, Matthews & Muir, 1980; Roll & Vedel, 1982; Cody, Schwartz & Smit, 1990).

Relation to small-range high sensitivity of muscle spindles

It has been amply shown in animal experiments that muscle spindle afferents may be much more sensitive to small movements than to large movements (Matthews & Stein, 1969; Hasan & Houk, 1975*a*, *b*; Cussons *et al.* 1977; Hulliger *et al.* 1977). It may be questioned whether the responses to discontinuities found in the present study were dependent on the small-range high sensitivity as

studied in the cat. The average step size of the 8–10 Hz discontinuities in the present study would be of the order of 0·13 mm in terms of tendon excursion (Edin & Vallbo, 1990*a*) which seems to fall within the high sensitivity range if one extrapolates from studies on cat triceps surae muscles. However, such extrapolations to the present experiments on human finger muscles are uncertain for a number of reasons. Moreover, it has been shown that the high sensitivity is much degraded during on-going large movements, except when the movement is very slow (Baumann & Hulliger, 1991). Hence it is far from clear that the responses to the discontinuities of the present study are dependent on the high sensitivity range of the muscle spindles.

Arguments against stretch reflex origin of 8–10 Hz discontinuities

A reasonable hypothesis is that the 8–10 Hz discontinuities are accounted for by the spinal stretch reflex considering that the loop time of the monosynaptic stretch reflex is roughly twice the time period of the discontinuities. Moreover, the high proportion of muscle afferents responding to the discontinuities implies a massive proprioceptive input, primarily in the lengthening antagonist muscle. Oscillations in the spinal stretch reflex loop have also been advocated as the mechanism for physiological tremor during position holding (Lippold, 1970; Hagbarth & Young, 1979; Young & Hagbarth, 1980). However, accurate analyses of the time relations between the Ia afferent volley and reflex response failed to support this hypothesis for the discontinuities during movement because it was found that the temporal scatter of the afferent activity was very large and the reflex latency was too long to fit a cycle time of 100–120 ms.

These points were analysed further by modelling the time course of the response of a hypothetical Ia population. The model units were all assigned a long-term variability that was an average of the recorded variability as presented in Fig. 7, while mean time lag of individual units was distributed among the model units as a Gaussian distribution fitted to the recorded means of Fig. 5. The simulated population response to a single discontinuity during a flexion movement was a broad modulation of afferent activity rather than a distinct burst. It seemed highly unlikely that the dispersed population response from the muscle spindles would produce the abrupt change in speed from a positive to the negative acceleration commonly observed in the 8–10 Hz discontinuities.

In order to estimate accurately the spinal reflex latency, two sets of data were considered. First, the delay from Ia activity at the recording site to the increase of reflex EMG was estimated on the basis of available data for the H reflex in the long thumb flexor (m. flexor pollicis longus). Stimulation and recording sites for this reflex lie very close to the nerve and EMG recording sites used in the present study. The onset latency for this H reflex is not shorter than 16 ms, and the maximal reflex effect occurs a few milliseconds later, at around 20 ms (Deschuytere, Rosselle & De Keyser, 1976; Ongerboer de Visser, Schimsheimer & Hart, 1984). Second, the electromechanical delay from muscle activation to change in acceleration in the present system is accurately estimated in the cross-correlation analysis, i.e. 19 ms. The total delay from recorded Ia activity to joint deceleration would then amount to 35–39 ms. Analysis of the kinematic pattern of typical discontinuities revealed, however, that the reflex response is too delayed to generate the observed kinematic pattern, because the peak deceleration commonly occurred some 15 ms earlier than would be predicted by the hypothesis.

Hence, the analysis of the time relations suggests that the monosynaptic stretch reflex cannot by itself cause the 8–10 Hz discontinuities. Other findings to be published in separate reports further support this interpretation.

On the assumption that the stretch reflex is the most powerful spinal mechanism responding to speed variations, the present analysis seems to be more consistent with the interpretation that 8–10 Hz discontinuities are accounted for by internal mechanisms within the central nervous system, e.g. a pulsatile component of the descending motor command, rather than by a reflex modulation at the spinal level. This interpretation might have interesting implications with regard to central as well as proprioceptive mechanisms in the control of voluntary finger movements.

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