

LONG-LATENCY STRETCH REFLEXES AS CO-ORDINATED FUNCTIONAL RESPONSES IN MAN

By C. C. A. M. GIELEN*, L. RAMAEKERS AND E. J. VAN ZUYLEN

*From the Department of Medical and Physiological Physics, University of Utrecht,
Princetonplein 5, P.O. Box 80 000, 3508 TA Utrecht, The Netherlands*

(Received 6 January 1988)

SUMMARY

1. Reflex activity in human arm muscles has been measured in response to torque perturbations around the elbow joint in the flexion–extension direction and/or the supination–pronation direction. Intramuscular fine-wire electrodes were used to record electromyographic (EMG) activity in the muscles. A pre-load was applied in the same direction as or in a different direction to the perturbation. The subjects were instructed to ‘hold on’, which means that they had to actively resist the perturbation without unduly co-activating their muscles.

2. The EMG activity showed segmented reflex responses with short-latency (25–50 ms) and long-latency (50–75 ms) components, followed by other bursts of activity which probably originated from the subject’s voluntary or triggered reactions.

3. Motor units in *m. triceps* gave short-latency and long-latency responses to imposed elbow extension but only long-latency responses were seen to imposed pronation, which does not stretch *m. triceps*. Motor units in *m. brachialis* gave short-latency and long-latency excitatory (inhibitory) responses to imposed extension (flexion) torques. However, only long-latency inhibitory responses were observed to imposed pronation torques. Motor units in *m. biceps* gave short-latency and long-latency excitatory responses to imposed pronation torques.

4. These results show that the long-latency reflex cannot be the result of a simple feed-back mechanism that controls muscle length only. We argue that the long-latency reflex activity reflects the co-ordinated activation of muscles which is necessary for an adequate response. This hypothesis is supported by the fact that the distribution of long-latency reflex activity over muscles was found to be similar to the distribution of activation found during a voluntary exerted torque in the direction opposite to the applied perturbation.

INTRODUCTION

When the position of a limb is disturbed, segmented EMG responses can be observed in the muscles that are stretched. Research concerning this reflex activity

* Present address: Department of Medical Physics and Biophysics, University of Nijmegen, Geert Grooteplein Noord 21, NL 6525 EZ Nijmegen, The Netherlands.

The authors’ names are in alphabetical order.

often concentrates on the function and origin of the long-latency component. This component follows the short-latency component, which, as most authors agree, originates from a monosynaptic excitation of motoneurons by Ia afferents from the stretched muscle. After still longer latencies (i.e. latencies exceeding 75 ms) triggered or voluntary reactions can be observed in the EMG signal. The origin of the long-latency component is controversial. A review of possible pathways mediating the different reflex components and their functional implications can be found in Houk & Rymer (1981).

Houk (1976) has argued that the stretch reflex gives rise to spring-like behaviour of the musculo-skeletal system. He states that the stiffness of the limb, counteracting external perturbations, is regulated by the incorporation of stretch reflexes (see Vincken, Gielen & Denier van der Gon, 1983). This idea implies that stretch reflexes effectively oppose perturbations.

We will address the question of whether or not the various components of the stretch reflex do indeed contribute to an adequate response to a perturbation. This is not a trivial question as will appear on closer inspection. When a pronation torque is applied to the forearm of a subject the muscles that make a torque contribution in the supination direction (i.e. *m. supinator* and *m. biceps brachii*) will be stretched. This implies that a stretch reflex can be expected in both muscles and a counteracting supination torque will be generated. However, this response will be inadequate because *m. biceps* will also exert a torque in the flexion direction. The reflex would therefore also lead to an undesired movement component in the flexion direction. Therefore, an adequate co-ordinated response cannot result from homonymous monosynaptic projections from muscle receptors to motoneurons alone. However, it is a well-known fact that there are heteronymous monosynaptic projections to synergistic muscles (Fritz, 1981; Stuart, Rymer & Schotland, 1986).

It has been suggested in the literature that the most important function of the short-latency component is to compensate for muscle yielding due to the breaking of actin-myosin bonds in stretched muscles (Allum, Mauritz & Vögele, 1982; Allum & Mauritz, 1984). This indicates that the short-latency reflex component may not be responsible for a co-ordinated response, which leaves the long-latency reflex as a possible candidate. We therefore propose as a working hypothesis that the muscles acting around a joint will be activated in the long-latency reflex in the same way as during a voluntary contraction that would counteract the perturbation. Then, if a pronation torque perturbation is applied, a counteracting supination torque will be generated by the reflex-induced activation of not only the *m. supinator* and the *m. biceps* but also of the *m. triceps*. The activation of the latter counteracts the flexion torque exerted by the *m. biceps* in a voluntary contraction in the supination direction (van Zuylen, Denier van der Gon, Gielen & Jongen, 1986; van Zuylen, Gielen & Denier van der Gon, 1988). If this hypothesis is correct *m. triceps* that is not stretched by the pronation perturbation should show increased activity in the long-latency reflex component. This is one of the predictions that we have tested in this study.

Another interesting situation arises if a pronation perturbation is imposed while a flexion torque, which includes the activation of the *m. brachialis*, is being voluntarily exerted by the subject. In this situation, a voluntary supination torque would

require the activation of the m. supinator and the m. biceps together with the m. triceps but in this case in combination with a reduction of the activation of the m. brachialis (van Zuylen *et al.* 1988). So, the second prediction that we will test in this study is that there is a reduction of activity in the m. brachialis at long latency when a pronation perturbation is added to an extension pre-load. The reduction of activity should be there even though this muscle is not shortened by the perturbation.

To check the validity of these predictions, we performed experiments on human subjects by imposing load perturbations at random moments in various directions, superimposed on pre-loads in different directions.

METHODS

Experimental protocol

Experiments were performed on five normal subjects, who gave their informed consent. The subject was comfortably seated in an adjustable dentist's chair. The right arm was slightly abducted in a horizontal plane and supported under the elbow joint. The angle between upper arm and the frontal plane was about 25 deg. The angle between upper arm and forearm was about 90 deg. The wrist was kept in the neutral position between full supination and full pronation.

The wrist of the subjects was fixated in a metal holder by means of a plaster cast. The plaster cast reduced any movements of the wrist in the holder to less than 0.2 deg in the flexion-extension direction and to less than 3 deg in the supination-pronation direction. The metal holder could be fixated to a device which allowed movements in the flexion-extension and supination-pronation direction, such that the axes of rotation for flexion-extension and supination-pronation of the apparatus coincided with the anatomical axes of rotation of the arm.

With two torque motors torques could be exerted independently and simultaneously in the flexion-extension direction and in the supination-pronation direction. During an experiment with constant pre-load torque was generated in a particular direction. This pre-load was chosen slightly above the threshold for tonic firing of motor units so that following a perturbation, reflex activity with different latencies could be expected (Calancie & Bawa, 1985; see also Discussion). At random times the torque motors generated a torque perturbation with a duration of 200 ms in the same direction as or in a different direction to the pre-load. The duration was sufficient to elicit short-latency as well as long-latency reflexes (Wadman, Boerhout & Denier van der Gon, 1980). Torque perturbations as well as pre-loads in the flexion-extension direction ranged up to 12.5 N m. In the supination-pronation direction torques up to 3 N m were used. The interstimulus interval between subsequent torque perturbations varied randomly in the range 750–1000 ms. The perturbations could be either a selected combination of torques in the flexion-extension and supination-pronation direction or a sequence of these separate torque components in random order. The subject was instructed to 'hold on' (Hammond, 1956), meaning that the subject had to actively resist the perturbation without previously co-activating the muscles.

The position of the forearm in both directions was measured by means of two potentiometers with a resolution of 0.1 deg. The position in the supination-pronation direction is given as the difference between the actual angle and the angle in the neutral position. This neutral position was between full supination (about +90 deg) and full pronation (about -90 deg). In the flexion-extension direction the position is given as the angle between the upper arm and the forearm. Full extension corresponds to 180 deg. EMG signals from m. biceps, m. triceps and m. brachialis and the signals of the position in both directions were stored on an analog FM tape-recorder (Honeywell, type 101) for off-line analysis. On a separate channel of the tape-recorder an identification signal was recorded to indicate the onset and direction of the perturbation torque. This signal was generated by the microprocessor which controlled the experiments.

EMG recording

Nylon-coated fine-wire electrodes (diameter 25 μm ; material; Karma, Californian Fine Wire Company) were inserted with the help of a hollow needle (diameter 0.4 mm) that was extracted after the wires had been inserted. The EMG signals were processed in two different ways. To

analyse motor-unit activity, bipolar recordings from wires which had a small recording area were amplified and bandpass-filtered (typically 320 Hz–32 kHz). Typically recordings were obtained from a single or from a few (2 or 3) motor units. In the latter condition a single motor unit was active in the pre-stretch period and two or three motor units contributed to the reflex activity. With a window trigger, a delay line and a large-screen oscilloscope we selected the action potentials of motor units that could easily be distinguished from other action potentials in the EMG recording. We made sure that we were recording from the same motor units throughout an entire experiment by continuously monitoring the shape of the action potentials.

In other experiments we measured multi-unit activity, i.e. the activity from five units or more. For this purpose we used fine-wire electrodes from the tip of which a few millimetres of the insulation had been removed. In this way the behaviour of a larger number of motor units was recorded simultaneously. The signals were amplified and bandpass-filtered but now in a lower frequency range, namely from 60–600 Hz.

In two experiments we were not completely sure whether the motor units that we recorded from were located in the lateral part of the m. biceps or in the m. brachialis. In later experiments we used electrical stimulation to identify the muscle from which motor-unit activity was recorded via the same wire electrodes.

Off-line analysis

A post-stimulus time histogram (PSTH) was constructed in order to study the average response of motor units to a torque perturbation. The identification pulses from the tape which indicate the start of the perturbation were used to start a digital averager. With the help of the window trigger we selected the action potentials of a particular motor unit. The trigger pulses were fed to the averager to evaluate the probability of firing before the stimulus. Every event (motor unit action potential) was counted in bins with a typical bin width of 3 ms. We made certain that the choice of the duration of the bins was not critical for the results. Increasing the bin width up to 7 ms had no systematic influence on the significance of results. In general the EMG signal was delayed for 50 ms in order to obtain a pre-trigger signal. In that way we could find out the average firing probability of the selected motor unit before the perturbation. Sometimes there were more than one motor unit in the EMG recording that caused a trigger pulse after the perturbation. Between 150 and 400 responses were used for averaging over a period of 256 ms. The bin counts before the perturbation were analysed with Poisson statistics (Cox & Lewis, 1966). With this procedure we can give two-sided confidence levels (for instance for $P = 0.05$) within which the number of events per bin is supposed to fall if no influence of a perturbation on the probability of firing is present. The choice of $P = 0.05$ indicates that an aberrant count of events can be expected to occur about once every twenty bins. Therefore, we were careful with the interpretation when the confidence level was crossed in a single bin only. For instance in Fig. 3B the number of events in the bin corresponding to a latency of 40 ms was not considered to be due to reflex activity because the bins on each side did not support this conclusion. However, if the confidence level was exceeded in two or more subsequent bins, this was considered to be significant.

The multi-unit recordings were analysed in a similar way. The EMG signal from the tape was rectified and averaged following the stimulus. Usually, a bin width of 1 ms was used in this case. We used Gaussian statistics to find the average level and the $P = 0.05$ confidence levels for the multi-unit EMG signal before the stimulus.

RESULTS

General description of results

The reflex responses in this study were frequently segmented, consisting of separate peaks (or troughs). The first component most often had a latency of about 25 ms and the second component a latency of 50 ms or above (e.g. Figs 1 and 2). We have therefore defined short-latency reflexes as those occurring between 25 and 50 ms and those in the range 50–75 ms as long latency (sometimes also referred to as medium latency in other studies). The reflex component arriving after about 50 ms

is also called the medium-latency reflex in other studies. The latencies reported are slightly longer than those usually reported in the literature. A possible explanation may be that the accelerations induced by the torque motors were rather slow (see Fig. 1 and Discussion). Components arriving later than 75 ms after the perturbation have not been taken into consideration for two reasons. In the first place it is possible that voluntary reactions of the subject to the perturbation start to play a role (Hammond, 1956; Crago, Houk & Hasan, 1976). In the second place the position trace in the supination-pronation direction changes its direction at about 100 ms after the perturbation, as shown in Fig. 1*B* and *C*. This overshoot in the position trace is part of the oscillations which originate due to the underdamped bio-mechanical properties of the forearm for movements in the supination-pronation direction.

In Figs 1, 2, 3 and 4 typical examples are given of the results. In the upper part of Fig. 1*A*, *B* and *C* and in Fig. 3*A*, *B* and *C* and in Fig. 4 the number of action potentials per second is given as a function of time. The three horizontal lines indicate the average number of events per bin and the confidence levels for $P = 0.05$. An example of the position of the arm following a perturbation is shown in the lower two traces of Fig. 1*A*, *B* and *C*. These position traces were obtained by averaging the position signals following the perturbation. These responses showed very little variability. The upper position trace in Fig. 1*A* shows that the elbow angle changes, starting at the onset of the perturbation in the flexion direction. The lower position trace shows that a torque perturbation in the flexion-extension direction has no effect on the position in the supination-pronation direction. Figure 1*B* and *C* shows the responses to a perturbation including a component in the pronation direction.

Figure 2 shows an analysis of a multi-unit recording. With respect to the existence and latencies of the different reflex components the results are similar to the results obtained with single-unit analyses.

Testing of the hypothesis; reflexes in non-stretched muscles

M. triceps. In seventeen experiments on five different motor-unit recordings in three different subjects we confirmed that motor units of the *m. triceps* respond with an increase in the probability of firing at short latency and long latency after a perturbation torque in the flexion direction. All motor units in *m. triceps* found in this study belonged to the subpopulation of motor units with a recruitment threshold that depends on torques both in the extension and supination direction (see van Zuylen *et al.* 1988). This was true both for the motor units that were active before the perturbation, as well as for the motor units that were recruited by the perturbation. In Fig. 1*A* results of a typical experiment are shown. Multi-unit activity was analysed in two additional experiments performed on one of the three subjects under similar conditions (see Fig. 2*A*). The latency of the short-latency component, averaged for all results, was 31 ms (s.d. = 2 ms). The latency of the long-latency component was on average 56 ms (s.d. = 4 ms).

In seventeen experiments, including the same five motor-unit recordings mentioned above, we measured motor-unit activity following a perturbation in a pure pronation direction, which does not stretch the *m. triceps*. In two additional experiments multi-unit activity was analysed in the same condition. The muscle was

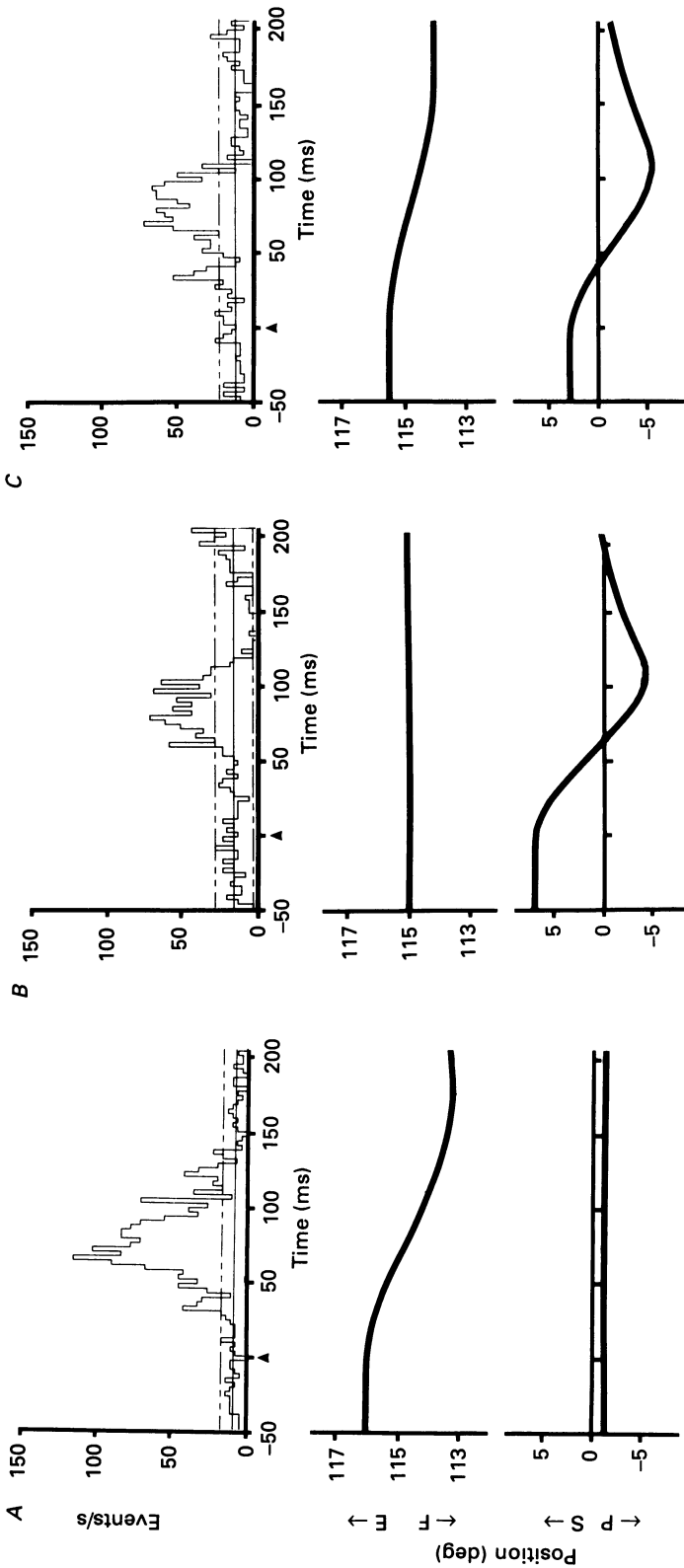


Fig. 1. Post-stimulus time histograms (PSTHs) which reveal the response of motor units in the m. triceps to perturbations with a duration of 200 ms in different directions together with the corresponding positions of the wrist in the flexion-extension (F-E) direction in the supination-pronation (S-P) direction. Averaged motor-unit activity is shown in the time interval between 50 ms before to 206 ms after the perturbation. In these experiments the m. triceps counteracts a flexion pre-load of 5.9 N m. The arrows indicate the start of each perturbation ($t = 0$). In each PSTH three horizontal lines have been indicated. The continuous line gives the average number of events per second before the perturbation. The interrupted lines give the confidence levels for $P = 0.05$ based on the activity of the motor unit before the perturbation. *A*, average response to 104 perturbations of 5.2 N m in the flexion direction. The elbow angle changes about 3 deg in the flexion direction and the m. triceps is stretched. A relatively small short-latency response at about 30 ms is followed by a much larger long-latency response which starts at about 47 ms. *B*, average response to 130 perturbations of 1.3 N m in the pronation direction superimposed on a flexion pre-load. The m. triceps is not stretched by this perturbation; this can be concluded from the flexion-extension position trace. There is no significant short-latency response. The activity is significantly increased starting at about 60 ms. *C*, average response to 119 perturbations of 3.3 N m in the flexion direction combined with a perturbation of 0.9 N m in the pronation direction, both superimposed on the same flexion pre-load as used in *A* and *B*. The stretch of the m. triceps, caused by the flexion movement, is reflected in the short-latency response. At long latency an increased activity can be observed which might originate from the stretch in the flexion direction as well as from the perturbation in pronation direction.

voluntarily activated to counter a pre-load of a combination of flexion and pronation torques. In all cases we found a significant increase in the EMG activity (see Figs 1 *B* and 2 *B*). The average latency of this increased activity is 61 ms (S.D. = 4 ms) and is therefore classified as a long-latency response. At short latency in general no significant increase or decrease was present. In two experiments exceptions were found; these recordings showed an increased EMG activity that started as early as about 20 ms after the perturbation. This latency is very short compared to the

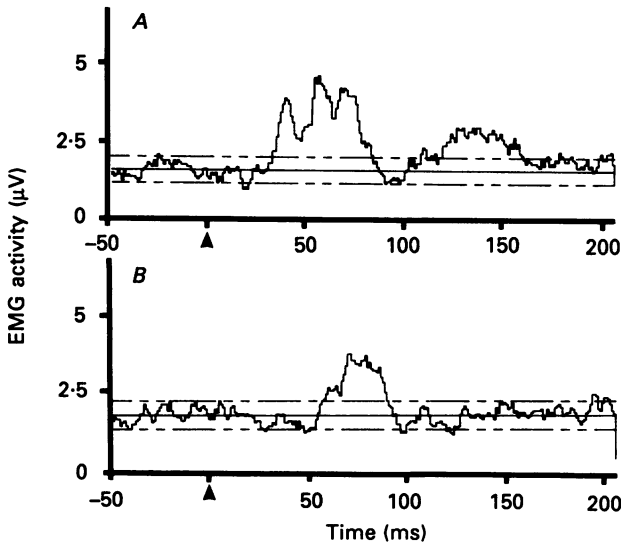


Fig. 2. Average rectified multi-unit EMG activity of the *m. triceps* in the period between 50 ms before and 206 ms after the perturbation. The arrow indicates the start of the perturbation ($t = 0$). The *m. triceps* is activated voluntarily to counteract a pre-load of 0.7 N m in the flexion direction. The average level of activity before the perturbation (continuous line) and 0.05 confidence levels are indicated in each figure. *A*, average response to 221 perturbations in the flexion direction of 2.0 N m. The activity is significantly increased starting at about 34 ms (short latency) which is clear from the fact that the 0.05 confidence level is crossed at that time. A second burst of activity starts at about 50 ms. This long-latency response consists of two peaks. However, the splitting in two peaks was not a systematic finding. *B*, average response to 267 perturbations of 0.7 N m in the pronation direction which does not stretch the *m. triceps*. At about 17 ms the activity starts to be significantly increased.

latency of short-latency responses found in the other experiments. We do not have an explanation for the exceptions. The aberrant responses were not reproducible and the EMG recordings did show a behaviour that corresponds to the hypothesis in all other experiments under the same conditions. In Table 1 an overview is given of the number of EMG recordings tested and the results obtained using a pure pronation perturbation.

The findings described above were confirmed in experiments in which pronation torques were combined with torques in other directions. The direction of the perturbation could be changed from pure flexion to pure pronation and different combinations were studied in between and in random order. When the amplitude of

the pronation perturbation was increased simultaneously with decreasing the amplitude of the flexion perturbation (see Fig. 1C), the responses changed from a reflex with a short-latency and a long-latency component to a response with a long-latency component only.

In five experiments we also applied extension torque perturbations in combination with either flexion pre-loads (thereby temporarily lowering the torque that had to be exerted by the subject) or in combination with pre-loads in the pronation direction.

TABLE 1. The number of times a particular behaviour was observed after a pure pronation perturbation at either short or long latency

Sign of the response	M. triceps		M. brachialis	
	Short latency	Long latency	Short latency	Long latency
+	0	7†	0	0
+ / 0	2	0	1	0
0	5†	0	5 + 2*†	0
- / 0	0	0	0	1
-	0	0	0	5 + 2*†

Motor units in m. triceps (m. brachialis) were tested with pre-loads in the flexion and pronation (extension and pronation) direction. All motor units in m. brachialis were of the type with a recruitment threshold for flexion that decreased when supination torque increased (see van Zuylen *et al.* 1988). Each recording was tested at least twice. † indicates the prediction based on the hypothesis. The sign of the reflex component shown in the first column indicates whether the activity at short or long latency is systematically greater (+) or smaller (-) than the pre-stimulus activity or if there is no difference (0). The arrays indicated by + / 0 and - / 0 summarize the results of EMG recordings with an aberrant behaviour in one particular test-run, whereas all other experiments on the same EMG recordings confirmed the hypothesis. The asterisks indicate that two recordings which were classified as belonging to the m. brachialis might have been obtained from the lateral part of the long head of the m. biceps.

In these experiments we consistently found a significant decrease in the firing probability at short latency and long latency (Evarts & Granit, 1976). The latency of the decrease at short latency was on average 35 ms (s.d. = 4 ms). In the long-latency period the level of activity was significantly less than the pre-stimulus level. It is difficult to give an average latency for this response, because the activity generally remained low from short latency on and did not regain the original pre-stimulus value (see section m. brachialis and Fig. 4).

M. brachialis The m. brachialis was tested in eighteen experiments on eight different motor-units recordings following muscle stretch caused by a pure extension perturbation torque that was superimposed on an extension pre-load. Motor-unit recordings were obtained for four subjects. All motor units in m. brachialis in this study belonged to the subpopulation of motor units with a recruitment threshold for flexion that increases if supination torques are exerted simultaneously (see van Zuylen *et al.* 1988).

It was confirmed that when the muscle was stretched an increase of EMG activity is present at short latency and at long latency. The average latency of the short-latency response was 28 ms (s.d. = 1 ms). The average latency of the long-latency response was 52 ms (s.d. = 2 ms). An example of these findings is given in Fig. 3A.

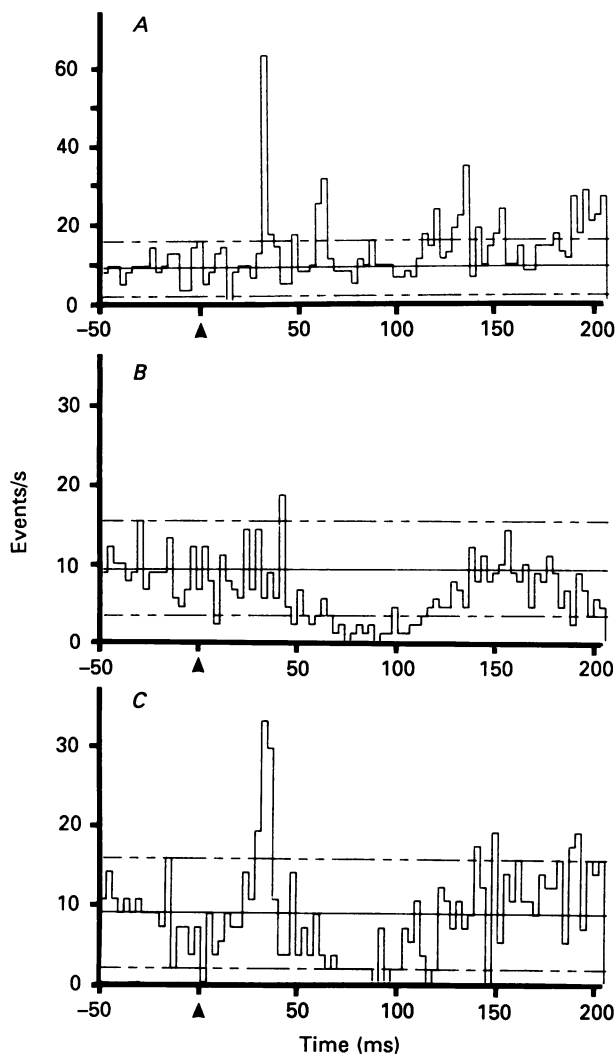


Fig. 3. Response of a single motor unit in the *m. brachialis* to perturbations in extension and/or pronation direction represented by PSTHs. The arrows at $t = 0$ give the onset of the perturbation. The *m. brachialis* is activated voluntarily to counteract a pre-load of 3.3 N m. Averaged number of events before the perturbation (continuous line) and confidence levels ($P = 0.05$; interrupted lines) are indicated. Note that the vertical axis in *A* is different from the vertical axes in *B* and *C*. *A*, average response to 213 extension perturbations of 2.0 N m which stretch the *m. brachialis*. A high probability of firing is observed at short latency at 30 ms. At 60 ms the activity is again increased significantly, although this response is rather small. *B*, average response to 305 perturbations of 0.7 N m in the pronation direction. The muscle is not stretched or shortened following the perturbation. The small peak at 40 ms is not considered to be significantly different from the pre-stimulus activity for reasons mentioned in the Methods. Between 50 and 65 ms the activity is significantly decreased. *C*, average response to 191 perturbations of 1.3 N m in the extension direction combined with a perturbation of 0.7 N m in the pronation direction. An increased activity at short latency is followed by a decrease in the activity at long latency, which starts at 50–70 ms. Although the $P 0.05$ confidence level is not crossed in this interval it can be concluded that the activity of this motor unit is certainly lower than the average value in the pre-stimulus interval.

When an extension pre-load was combined with flexion torque perturbations (thereby lowering the pre-load) unloading responses were found. The average latency of the decrease at short latency was 31 ms (s.d. = 2 ms). The onset of the long-latency component could not be established accurately for reasons explained before for the m. triceps. A typical example of an experiment including unloading perturbations is shown in Fig. 4.

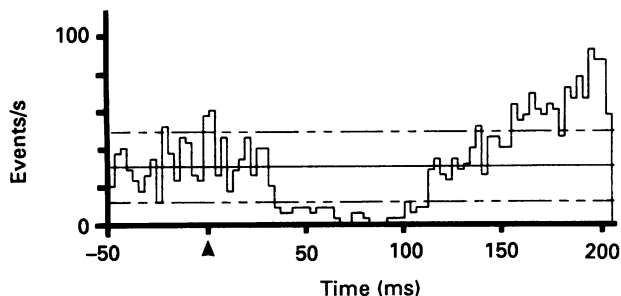


Fig. 4. Average unloading response of a single motor unit of the m. brachialis to 120 perturbations of 2.0 N m in the flexion direction. The muscle was activated voluntarily to counteract an extension pre-load of 2.9 N m. At about 30 ms the activity of this motor unit decreases. The activity remains low also during the long-latency period.

Experiments including a pronation torque perturbation were performed 24 times on the same eight motor-unit recordings which were mentioned above, to test the second prediction of the hypothesis, as given in the Introduction.

In Fig. 3*B* the response to a pure pronation torque perturbation is expressed as a function of time. At short latency the probability of firing is not considered to be significantly different from the mean probability of firing before the perturbation because of the fact that the significance level is crossed only in a single bin (see Methods). The other recordings tested did not show such an occasional deviation at short latency. This is to be expected if we assume that short-latency reflexes occur in stretched muscles only. At long latency, however, the probability of firing is clearly decreased, the decrease starting 50 ms after the onset of the perturbation. In the experiments performed on other subjects we generally found that the latency at which the probability of firing decreased significantly was greater than the latency of the increases found at long latency when the muscle was stretched. The average latency for the decrease in activity at long latency as 64 ms (s.d. = 7) ms. The results of experiments which include pure pronation torque perturbations are summarized in Table 1.

In Fig. 3*C* the response of the same motor-unit recording is shown for a combination of perturbations in the extension and pronation direction. The response looks very much like the summed responses shown in Fig. 3*A* and *B*. The muscle is stretched by the perturbation in the extension direction; this is reflected in the short-latency reflex component. Nevertheless, at long latency a decrease in the firing probability is observed, which corresponds to the perturbation in the pronation direction.

In one particular test-run a motor unit in the m. brachialis showed an aberrant

behaviour. At short latency after a torque perturbation in the pronation direction a significant increase in the firing probability was observed and at long latency the firing probability was not significantly different from the firing probability before the stimulus. However, this behaviour could not be reproduced and this motor unit responded to other pronation perturbations similarly as the other motor units in *m. brachialis*.

As mentioned in the Methods, we were not sure for two motor-unit recordings whether they were from the *m. brachialis*. In these experiments our intention was to insert the wires into the lateral part of the *m. biceps*, which borders on the *m. brachialis*. We confirmed that these motor units were not activated during voluntary contractions in the supination direction. However, this finding holds for the 'flexion motor units' of the *m. biceps* as well as for motor units of the *brachialis* (ter Haar Romeny, Denier van der Gon & Gielen, 1984; van Zuylen *et al.* 1986, 1988). The two motor units, tested in a total of nine experiments which included pronation perturbations, did behave like the motor units of the *m. brachialis* and were therefore classified as belonging to the *m. brachialis*; when subjected to a pronation perturbation they did not show a short-latency reflex and their activity was decreased at long latency.

M. biceps. Our hypothesis is that long-latency reflex activity is elicited in *m. triceps* by torque perturbations in the pronation direction in order to compensate for the torque component of *m. biceps* to torque in the flexion direction. If this is true, it would be interesting to see whether reflex activity is induced in *m. biceps* under the same experimental conditions as used to test *m. triceps*. The experiments on motor units in *m. triceps* were done with a flexion pre-load, loading the extensor muscles. In these conditions *m. biceps* is relaxed. Three experiments have been done on three subjects. In one experiment we could record single-motor-unit activity. In the other two experiments multi-unit activity was recorded. All three experiments gave the same results.

Figure 5 clearly shows reflex activity of a motor unit in *m. biceps* (*caput longum*) at short latency and at long latency. This motor unit belongs to the subpopulation in *m. biceps*, the recruitment threshold of which depends on torques both in the flexion and supination direction (ter Haar Romeny *et al.* 1984). The activity of the motor unit shown in Fig. 5 was recorded in the same experimental conditions as those of the motor units in *m. triceps* shown in Fig. 2*B*. These units in *m. triceps* showed clear reflex activity at long latency but revealed no short-latency reflex activity, just as illustrated in Fig. 2*B*. The few bins with an action potential in the pre-stretch period in Fig. 5 are due to the fact that motor units in *m. biceps* have a much lower recruitment threshold than recruitment threshold (see Denier van der Gon, ter Haar Romeny & van Zuylen, 1985). This means that motor units in *m. biceps* with a low recruitment threshold may not yet have stopped firing completely after the previous stretch in some conditions. Therefore, a small co-contraction was present even though the subject was instructed to relax completely after each stretch.

In general it was much easier to elicit reflex activity in motor units that were already active in the pre-stretch period than in motor units that were not active before the torque perturbation. This suggests that the amplitude of the long-latency reflex activity in *m. triceps* to torques in the pronation direction may depend on

whether m. biceps is active prior to the torque perturbation since the activity in m. triceps is thought to compensate for the flexion torque component generated by the reflex activity in m. biceps. Although our data do not allow any statistically significant conclusions to be made, there seemed to be a tendency for the long-latency reflex activity in m. triceps to increase if a pre-load in the pronation direction was added to that in the flexion direction.

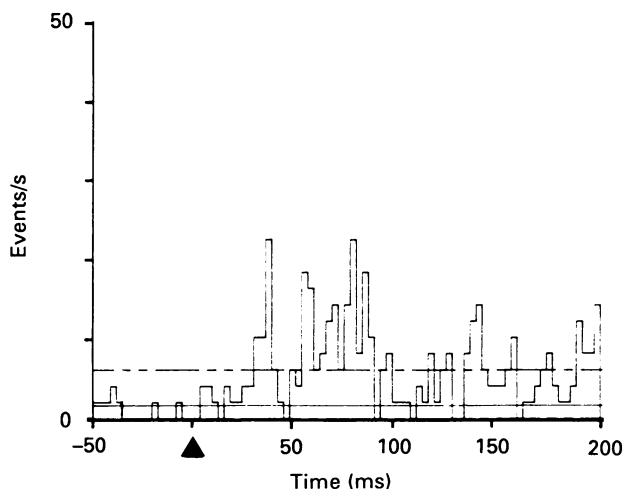


Fig. 5. Post-stimulus time histogram obtained by averaging of single-motor-unit activity in m. biceps to torque perturbations of 0.7 N m in the pronation direction, superimposed on a flexion pre-load of 0.7 N m. The arrow at $t = 0$ indicates the onset time of the perturbation.

Superposition of perturbations

The average latency for short-latency responses in the m. biceps following stretches caused by perturbations in the extension and pronation direction was 25 ms (s.d. = 2 ms) and for the long-latency component 50 ms (s.d. = 4 ms). We found that when torque perturbations in both directions were imposed simultaneously, the short- and long-latency reflex activity was much larger than in the separate cases. This may suggest that reflex activity originating from stretches in different directions is summed. Evidence for summation of responses also comes from the data shown in Figs 1C and 3C. However, we have not investigated this issue quantitatively in detail for all motor units.

The amplitude of the reflex components generally increased with the amplitude of the perturbation. We confirmed that when the pre-load was too low to keep a motor unit firing tonically the amplitude of the short-latency reflex component for this motor unit decreased significantly (Calancie & Bawa, 1985). The results of two motor-unit recordings are shown in Figs 1A and 3A; these are two extreme examples of this phenomenon. A motor unit of the m. triceps (Fig. 1A) fired very irregularly before the perturbation and now and then it even stopped firing during the experiment. A relatively high perturbation torque was applied. As a result of the too low pre-load a small response at short latency was found, whereas a large response was observed at long latency. This response included the reflex response of several

motor units which were not active before the perturbation. In the recording of the m. brachialis (Fig. 3A) one motor unit fired regularly and a relatively small perturbation in the extension direction was applied. This resulted in a high response at short latency, whereas the response at long latency was relatively small. This response only included action potentials of the previously active motor unit.

Unloading of m. biceps by torques in either the supination or flexion direction caused a decrease in the activity of motor units of the m. biceps at short latency as well as at long latency (Evarts & Granit, 1976). In this case the latency of the short-latency responses was 31 ms (s.d. = 3 ms) which is slightly longer than the latency of the short-latency response after an extension perturbation. This was also found for the other muscles when unloading responses were studied. Sometimes, when a decrease of long-latency reflex activity was found, slightly higher pre-loads had to be used to obtain significantly decreased activity than in experiments on the same EMG recording that elicited increased EMG activity. This was the case for unloading experiments as well as for the experiments on motor units of the m. brachialis with pronation perturbation.

DISCUSSION

General findings

In this paper we have presented the results of measurements of the distribution of the activation of motor units during reflex activity. This activity resulted from a torque perturbation which was applied to the forearm of the subject. Before the perturbation the arm muscles were activated voluntarily to counteract a pre-load. We have found that during perturbations in the flexion-extension direction and in the supination-pronation direction segmented EMG responses were elicited that are similar to reflex responses reported in the literature (for instance Hammond, 1956). The short-latency reflex was only found in muscles that have been stretched by the perturbation. Fritz (1981) showed that in the cat there are strong mutual heteronymous monosynaptic Ia projections between functional synergistic muscles in the forepaw. However, the design of the experiments here was generally inappropriate to reveal these synergies, though no doubt heteronymous projections were also involved in generating the short-latency reflexes that were seen (e.g. excitation of brachialis with an extension torque).

We have found that there is a great similarity between the distribution of activation at long latency and the distribution of activation during voluntary contractions (van Zuylén *et al.* 1986, 1988). This distribution of activation may cause a co-ordinated response to a perturbation. From the position traces in Fig. 1A and B we can conclude that no movements in the supination-pronation direction occur after a perturbation in the flexion-extension direction and vice versa. This indicates that the counteracting response may indeed have had the correct direction. Therefore, it implicitly supports our presupposition that a co-ordinated response is executed without deviations in unwanted directions.

Two separate findings lead us to the conclusion that there is a great similarity in the distribution of long-latency reflex activity and the activation during voluntary contractions. In the first place, there is increased EMG activity at long latency in

the m. triceps when a flexion or pronation pre-load is combined with a pronation perturbation, although the muscle is not stretched. This finding corresponds to the activation of the m. triceps in voluntary isometric contractions in the supination direction (van Zuylen *et al.* 1986, 1988). However, it is a remarkable finding when we take into account that m. biceps and m. triceps are generally considered to be antagonistic muscles. Ia inhibition takes place between two antagonistic forearm muscles in humans (Day, Marsden, Obeso & Rothwell, 1984). Secondly, there is a decrease in the EMG activity of the m. brachialis at long latency when an extension pre-load is combined with a pronation perturbation which does not stretch or shorten the muscle. Therefore, the decrease cannot be explained by a decrease of homonymous excitation originating from muscle spindles of the m. brachialis. However, it corresponds to the reduction in activation found in the m. brachialis when a voluntary supination torque is added to a voluntary flexion torque (van Zuylen *et al.* 1986, 1988).

Findings comparable to ours have been reported in the literature but the direct correspondence with voluntary activation is not mentioned. Such experiments did not include combinations of pre-loads and perturbations in different directions. Lacquaniti & Soechting (1986) mention that when the m. biceps and m. brachialis reflexes occur at long latency that are not strictly correlated to stretching or shortening of the muscle. These experiments were carried out in the condition of simultaneous disturbances around the shoulder and elbow joint. Traub, Rothwell & Marsden (1980) have reported that muscles of the thumb that are voluntarily activated to press a button may be activated at long latency although they are shortened by a stimulus that perturbs the position of the forearm. The findings show that the long-latency reflex plays a functional role in the co-ordination of reflex-induced movements.

Recently, Le Bozec, Evans & Maton (1987) found that the recruitment order of motor units in m. anconeus and m. triceps during reflex-induced activity was constant. This result led the authors to suggest that all elbow extensor muscles may be recruited as a single motoneurone pool following Henneman's size principle. Our findings indicate that this suggestion may be true for elbow extensor muscles but does not hold for all 'synergistic' muscle groups since torque perturbations in the pronation direction induced excitatory long-latency responses in m. biceps and inhibitory long-latency responses in motor units in m. brachialis.

Characteristics of the reflex activity

The latency of the short-latency component of the stretch reflex is slightly longer than the latency of the tendon jerk reflex which is found by using tendon taps. In the case of the biceps the tendon-jerk latency is at least 18 ms (Marsden, Merton & Morton, 1976; Wadman *et al.* 1980; our own observations), whereas we found that the latency of the short-latency component in the stretch reflex for the m. biceps is about 25 ms. This discrepancy is probably caused by the fact that it takes some time for the muscle to become stretched to some extent after the onset of the torque perturbation (Wadman *et al.* 1980). The onset of the long-latency component generally came about 25 ms after the short-latency reflex (Wadman *et al.* 1980). The variability in the onset time, however, was greater than for the short-latency reflex.

For the different muscles significantly different latencies were found for the different reflex components. These differences may well result from differences in the conduction time for afferent and efferent signals to and from the spinal cord.

The latency of the decreased EMG activity following an unloading perturbation and for the m. brachialis at long latency following a pronation perturbation was usually greater than corresponding latencies found for increases in EMG activity. These differences can be partly understood from the fact that the responses of primary muscle spindles are highly asymmetrical (Houk, Crago & Rymer, 1981). Shortening of a muscle causes much smaller changes in the firing rate of spindles relative to stretching. A finding similar to our results was reported by Cheney & Fetz (1984) who found that responses to torque perturbations which shortened muscles showed slightly longer latencies than responses to torque perturbations which stretched muscles.

The amplitude of the short-latency as well as the long-latency reflex in PSTH measurements depends upon the pre-load. Calancie & Bawa (1985) describe similar findings in human subjects. They stated that motor units that responded in the reflex but that were not firing tonically as a result of the imposed pre-load usually did not show any activity during the short-latency period but only at long latency. For this reason we took special care to ensure that the firing rate in the pre-stretch period was the same in all situations in which we did not expect a short-latency component but only a long-latency component. This situation existed for example when we studied motor units in the m. triceps after a perturbation in the pronation direction. First, we compared these situations with perturbations in another direction that did cause a short-latency component. In the case of the mentioned example, this would mean a flexion perturbation. The pre-loads used in both conditions were the same or were adjusted if necessary in order to keep the firing rate in the pre-stretch period constant. Thereby we excluded the possibility that the absence of the short-latency component could be attributed to the fact that motor units were not firing tonically in the pre-stretch period. In the second place we performed experiments in which the activity of many motor units was recorded simultaneously. In the EMG signal from such a multi-unit recording some motor units were always tonically activated because of the pre-load.

Implications for existing models on the origin of long-latency reflexes

Matthews (1984) has presented evidence that the long-latency reflex depends upon responses of secondary muscle spindle afferents. Kirkwood & Sears (1974) have shown that secondaries project monosynaptically to motoneurons. However, long-latency reflexes occur in muscles that are not stretched by the perturbation. This cannot be attributed to the activity of secondaries unless additional assumptions are made. In the Introduction we followed the same line of argument in order to rule out the possibility that the short-latency response, originating from monosynaptic Ia projections, could give rise to a co-ordinated response. Furthermore, it is very unlikely that the reduction of activity at long latency in the m. brachialis after a pronation perturbation results from monosynaptic excitatory projections of muscle spindles.

Eklund, Hagbarth, Hägglund & Wallin (1982*a, b*) claim that mechanical oscil-

lations in stretched muscles cause afferent bursts which excite the motoneurone pool several times. Reasoning similar to that given above argues against the possibility that this is the complete explanation for our findings and thus for the origin of the long-latency reflex component.

An alternative explanation for the increased activity in the m. triceps at long latency after a pronation perturbation, instead of our suggestion, might be as follows. The central nervous system reacts to a suddenly increasing torque with an increased activation of all muscles around the joint. In that way the stiffness around the whole joint is increased by co-activation and the perturbation is counteracted, after which voluntary reactions take over. However, the finding that the activity of the m. brachialis is decreased at long latency after a pronation perturbation combined with a flexion pre-load argues against this explanation.

The function of the stretch reflex

The function of the stretch reflex has been the subject of intensive discussion in the literature. Our results show that the stretch reflex is not merely a length-regulating feed-back loop although it might add to a position feed-back mechanism. Houk and co-workers (Houk, 1976; Houk & Rymer, 1981) have argued that the stretch reflex serves to regulate the stiffness around a particular joint. When muscles are stretched, the perturbation is at first counteracted by passive forces (short-range stiffness). Then, at the moment when this passive force starts to decline, its role is taken over by reflex activity that opposes the yielding of the muscles. This yielding might even reduce muscle force below its pre-stretch level in the absence of the short-latency component (Allum *et al.*, 1982, 1984). Therefore, in stretched muscles the short-latency component is highly effective in stretched muscles in keeping up the force. As we have shown, short-latency reflexes occurred only in stretched muscles in our experiments. A longer latency is available for the co-ordinated response. During this extra time the long-latency reflex might be mediated by a supraspinal pathway or by an interneuronal spinal pathway, which incorporated afferent input of sources other than Ia afferents and influences of higher motor centres.

In conclusion, we can state that the long-latency reflex component is a highly flexible mechanism that might adequately serve to counteract perturbations in the correct direction.

We are grateful for the financial support of the Netherlands Organisation for the Advancement of Pure Research (Z.W.O.). We are also grateful to an anonymous reviewer whose suggestions improved the manuscript considerably.

REFERENCES

- ALLUM, J. H. J. & MAURITZ, K.-H. (1984). Compensation for intrinsic muscle stiffness by short-latency reflexes in human triceps surae muscles. *Journal of Neurophysiology* **52**, 797-818.
- ALLUM, J. H. J., MAURITZ, K.-H. & VÖGELE, H. (1982). The mechanical effectiveness of the short latency reflexes in the human triceps surae muscles revealed by ischaemia and vibration. *Experimental Brain Research* **48**, 153-156.
- CALANCIE, C. & BAWA, P. (1985). Voluntary and reflexive recruitment of flexor carpi radialis motor units in humans. *Journal of Neurophysiology* **53**, 1194-1200.

- CHENEY, P. D. & FETZ, E. E. (1984). Corticomotoneuronal cells contribute to long-latency stretch reflexes in the rhesus monkey. *Journal of Physiology* **349**, 249–272.
- COX, D. R. & LEWIS, P. A. W. (1966). *Statistical Analysis of a Series of Events*. London: Methuen.
- CRAGO, P. E., HOUK, J. C. & HASAN, Z. (1976). Regulatory actions of the human stretch reflex. *Journal of Neurophysiology* **39**, 925–935.
- DAY, B. L., MARSDEN, C. D., OBESO, J. A. & ROTHWELL, J. C. (1984). Reciprocal inhibition between the muscles of the human forearm. *Journal of Physiology* **349**, 519–534.
- DENIER VAN DER GON, J. J., TER HAAR ROMENY, B. M. & VAN ZUYLEN, E. J. (1985). Behaviour of motor units of human arm muscles: differences between slow isometric contraction and relaxation. *Journal of Physiology* **359**, 107–118.
- EKLUND, G., HAGBARTH, K.-E., HÄGGLUND, J. V. & WALLIN, E. U. (1982*a*). Mechanical oscillations contributing to the segmentation of the reflex electromyogram response to stretching human muscles. *Journal of Physiology* **326**, 65–77.
- EKLUND, G., HAGBARTH, K.-E., HÄGGLUND, J. V. & WALLIN, E. U. (1982*b*). The ‘late’ reflex responses to muscle stretch: the ‘resonance hypothesis’ versus the ‘long-loop hypothesis’. *Journal of Physiology* **326**, 79–90.
- EVARTS, E. V. & GRANIT, R. (1976). Relations of reflexes and intended movements. In *Progress in Brain Research*, vol. 44. *Understanding the Stretch Reflex*, ed. HOMMA, S. Amsterdam: Elsevier.
- FRITZ, N. (1981). Ia-synergismus an der vorderen Extremität der Katze. Thesis, Biology Faculty of the Ludwig-Maximilian-Universität München.
- HAMMOND, P. H. (1956). The influence of prior instruction to the subject on an apparently involuntary neuromuscular response. *Journal of Physiology* **132**, 17–18*P*.
- HOUK, J. C. (1976). An assessment of stretch reflex function. In *Progress in Brain Research*, vol. 44. *Understanding the Stretch Reflex*, ed. HOMMA, S. Amsterdam: Elsevier.
- HOUK, J. C., CRAGO, P. E. & RYMER, W. Z. (1981). Function of the spindle dynamic response in stiffness regulation – a predictive mechanism provided by nonlinear feedback. In *Muscle Receptors and Movement*, ed. TAYLOR, A. & PROCHAZKA, A. London: Macmillan.
- HOUK, J. C. & RYMER, W. Z. (1981). Neural control of length and tension. In *Handbook of Physiology*, vol. 1, II, *Motor control*, part 1, ed. BROOKHART, J. M. & MOUNTCASTLE, V. B., pp. 257–323. Bethesda, MD, U.S.A. American Physiological Society.
- KIRKWOOD, P. A. & SEARS, T. A. (1974). Monosynaptic excitation of motoneurons from secondary endings of muscle spindles. *Nature* **252**, 243–244.
- LACQUANITI F. & SOECHTING, J. F. (1986). Responses of mono- and bi-articular muscles to load perturbations of the human arm. *Experimental Brain Research* **65**, 135–144.
- LE BOZEC, S., EVANS, O. M. & MATON, B. (1987). Long-latency stretch reflexes of the human elbow extensors during voluntary relaxation: differences between antagonistic muscles. *Experimental Neurology* **96**, 516–527.
- LUNDBERG, A., MALGREN, K. & SCHOMBURG, E. D. (1987). Reflex pathways from group II muscle afferents. 3. Secondary spindle afferents and FRA: a new hypothesis. *Experimental Brain Research* **65**, 294–306.
- MARSDEN, C. D., MERTON, P. A. & MORTON, H. B. (1976). Stretch reflex and servo action in a variety of human muscles. *Journal of Physiology* **259**, 531–560.
- MATTHEWS, P. B. C. (1984). Evidence from the use of vibration that the human long-latency stretch reflex depends upon spindle secondary afferents. *Journal of Physiology* **348**, 383–415.
- STUART, G. J., RYMER, W. Z. & SCHOTLAND, J. L. (1986). Characteristics of reflex excitation in close synergistic muscles evoked by muscle vibration. *Experimental Brain Research* **65**, 127–134.
- TER HAAR ROMENY, B. M., DENIER VAN DER GON, J. J. & GIELEN, C. C. A. M. (1984). Relation between the location of a motor unit and its critical firing levels for different tasks. *Experimental Neurology* **85**, 631–650.
- TRAUB, M. M., ROTHWELL, J. C. & MARSDEN, C. D. (1980). A grab reflex in the human hand. *Brain* **103**, 869–884.
- VAN ZUYLEN, E. J., DENIER VAN DER GON, J. J., GIELEN, C. C. A. M. & JONGEN, H. A. H. (1986). Coordination of human arm muscles in flexion–extension and supination–pronation tasks. Part 1: Description of activation patterns. *Neuroscience Letters Supplement* **26**, S84.
- VAN ZUYLEN, E. J., GIELEN, C. C. A. M. & DENIER VAN DER GON, J. J. (1988). Coordination and

inhomogeneous activation of human arm muscles during isometric torques. *Journal of Neurophysiology* (in the Press).

VINCKEN, M. H., GIELEN, C. C. A. M. & DENIER VAN DER GON, J. J. (1983). Intrinsic and apparent muscle stiffness in man. *Neuroscience* **9**, 529-534.

WADMAN, W. J., BOERHOUT, W. & DENIER VAN DER GON, J. J. (1980). Responses of the arm movement control system to force impulses *Journal of Human Movement Studies* **6**, 280-302.