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DEPENDENCE OF AUTOGENIC AND HETEROGENIC STRETCH REFLEXES ON PRE-LOAD ACTIVITY IN THE HUMAN ARM

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SUMMARY

1. Subjects held their right arm in a horizontal plane. The angle of the elbow was 90 deg. They exerted forces in several directions in the plane of the arm, varying independently the pre-load torques about shoulder and elbow. We measured electromyographic (EMG) activity in several arm muscles in response to force perturbations which extended the shoulder, without changing the elbow angle.

2. The EMG activity in flexors of both shoulder and elbow showed reflex responses at short latency (≈ 25 ms). In all muscles the reflex activity increased with the pre-load activity of that muscle.

3. The short-latency reflex activity of m. brachialis, which was not stretched by the perturbations, was independent of the pre-load activity of the muscles acting over the shoulder.

4. From these results we conclude that the force resulting from the short-latency reflex, assessed from the EMGs, does not counteract the perturbations exactly. Having found that the short-latency reflex is dependent on the pre-load direction, we argue that this dependence makes the short-latency reflex suitable for correcting fast movements for misjudgments of load.

5. At longer latencies (> 50 ms) the direction of the force resulting from the reflex, assessed from the EMGs, was almost independent of the direction of the pre-load. In our experiment the force resulting from the long-latency reflex counteracted the perturbations quite well.

INTRODUCTION

Stretch reflexes are generally believed to counteract the perturbation that elicits them. The way in which the perturbation is counteracted is more controversial (Stein, 1982). If we consider a hinge-like joint, counteracting a perturbation requires only a response of the appropriate sign. If we consider a joint with more than one degree of freedom, or more than one joint, counteracting a perturbation requires a highly co-ordinated response. Little research has been done yet on the co-ordination of reflex activity when more than one degree of freedom is involved.

In the elbow joint the two degrees of freedom (flexion–tension and supination–pronation) are coupled by muscles like m. biceps which contributes to flexion as well as to supination. Gielen, Ramaekers & van Zuylen (1988) investigated the

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effect of this coupling on the co-ordination of the stretch reflex. If two or more separate joints are involved, inertial couplings complicate the co-ordination of the stretch reflex. To counteract for instance an extension of only the shoulder, a flexion movement of only the shoulder would be an adequate reaction. Due to the inertial coupling between upper and lower arm, this movement generally requires an activation of flexors of both elbow and shoulder, in a ratio dependent on the elbow angle. Thus an 'adequate' reflex in response to shoulder extension often has to include activation of elbow flexors. Lacquaniti & Soechting (1986*b*) did indeed report a 'short-latency' reflex in m. brachialis (a pure elbow flexor) in response to shoulder extension.

For fast goal-directed elbow flexion movements, Smeets, Erkelens & Denier van der Gon (1990*b*) have shown that adjustments in the electromyograph (EMG) could be observed about 35 ms after the nervous system had detected the unexpected load. These adjustments were observed at the same latency in muscles acting around the elbow as well as in muscles acting around the shoulder. The overall response was made approximately in the appropriate direction. This shows that there are conditions in which an adequate short-latency response is possible. The question that we would like to answer in the present study is whether the short-latency component of the stretch reflex is also an adequate response.

It is well known that the amplitude of the autogenic short-latency reflex increases roughly linearly with the activity in the muscle prior to the perturbation (Marsden, Merton & Morton, 1976; Wadman, Boerhout & Denier van der Gon, 1980; Matthews, 1986). On the other hand, to counteract a specific perturbation the direction of the reflexively induced reaction force has to be independent of the direction of the pre-load. Considering again the situation of an extension of the shoulder (without a change in elbow angle), we make two predictions on the basis of the hypothesis that the direction of the reflexively induced reaction force is independent of the direction of the pre-load.

The first prediction is that, since the reflex activity in shoulder flexors increases with the pre-load about the shoulder, the reflex activity in m. brachialis and m. biceps has to increase with the same pre-load. The second prediction on the basis of the hypothesis is that, since our results show that the reflex activity in the shoulder flexors is independent of the pre-load torque about the elbow, the reflex activity in m. brachialis and m. biceps must be independent of the pre-load torque about the elbow.

These predictions are tested experimentally in this paper. Preliminary results have been presented elsewhere (Smeets, Erkelens & Denier van der Gon, 1990*a*).

METHODS

Apparatus

The apparatus used in the experiment is described by van der Berg, Mooi, Denier van der Gon, Gielen & van der Meulen (1987). It consists of a horizontal rail along which a handle can be moved in a straight line over 0·5 m. The handle is attached to a metal belt which runs over two cogwheels. One of these is attached to a microprocessor-controlled torque motor and a digital position encoder. The handle can also be blocked mechanically for the performance of isometric experiments. Strain gauges built into the handle were used to measure the force exerted on the handle in three dimensions.

A horizontal array of LEDs placed over the rail was used to give the subjects information about either the hand position or the force exerted in the direction of the rail. The exerted force perpendicular to the rail in the plane of the arm was displayed as the vertical position of a line on an oscilloscope screen. No movement was possible perpendicular to the rail.

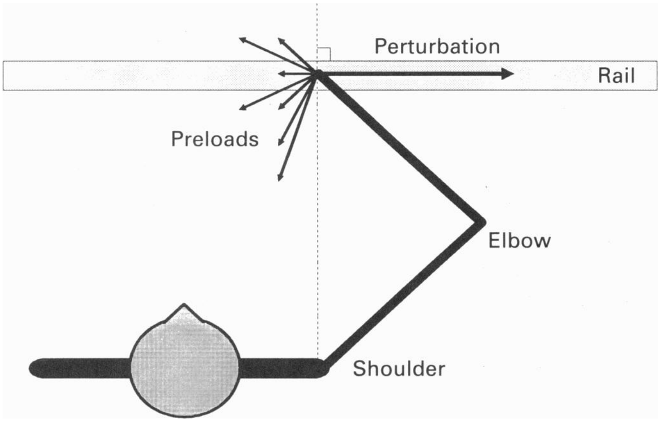

Fig. 1. Top view of the experimental configuration.

In the experiments EMGs were recorded from the following muscles: the shoulder flexor m. pectoralis major, the biarticular flexor m. biceps (both heads), the elbow flexor m. brachialis, and the elbow extensor m. triceps (lateral head). EMGs were recorded using bipolar Ag–AgCl surface electrodes, 0·6 cm diameter, placed 2 cm apart over the muscle bellies. Electrodes on m. brachialis were placed as far as possible from m. biceps, to prevent cross-talk from this muscle. The EMG signals were sampled after they had been band-pass filtered (16–320 Hz), rectified and low-pass filtered (10 ms). EMGs, handle position and three components of force were all sampled at 256 Hz and stored on disc.

Experimental procedure

The experiments, which have been approved by the Ethical Committee, were performed on seven healthy, right-handed subjects who had given informed consent. They sat on a chair holding their right arm in a horizontal plane. To relax the shoulder muscles, the arm was supported under the elbow joint. The wrist was supinated, immobilized and tightly strapped to the handle. Shoulder angle (θ_1) was about 45 deg (0 deg: upper arm in frontal plane); elbow angle (θ_2) was about 90 deg (0 deg: full extension). The rail was placed in such a position that its angle with the line through shoulder and hand was 90 ± 1 deg.

In this configuration (see Fig. 1), the movement along the rail caused initially only shoulder rotation. During the first 50 ms of the perturbation, the displacement of the hand was always less than 1 cm. Displacements of this amplitude induce a shoulder rotation of approximately 1·2 deg and an elbow rotation of less than 0·01 deg.

An experimental session generally consisted of five series of seventy-five force pulses that extended the shoulder. Three amplitudes (5, 7·5 and 10 N) of force pulses were presented in random order. The duration of the pulses was 100 ms. During each series the subject was asked to exert a force in the plane of the arm perpendicular to the rail at a prescribed level, and to oppose the pre-load force generated by the motor in the direction of the rail. Subjects were instructed not to react to the perturbations, and to let their hand move back to the starting position after the perturbation. The instruction 'do not intervene' was chosen to minimize the variability in the response and to prevent co-contraction. Subjects knew that all the perturbations would be in the same direction.

With each subject about five experimental sessions were carried out; in each session a different pre-load was used. To scan the possible combinations of torques, several different series of pre-loads were used.

Data analysis

Before each experimental session began an isometric EMG–force relation was determined. For this, the handle was blocked and the subject was asked to exert a force along the rail. With the help of the LED array ten target force levels were indicated, ranging from 0 to 50 N, which had to be matched by the subject. At each of these force levels the exerted forces and the four EMGs were sampled. From linear least-squares fits to these data, EMG–force relations were derived for the muscles around both joints. Using these relations for each muscle the EMGs can be expressed as a corresponding force exerted along the rail.

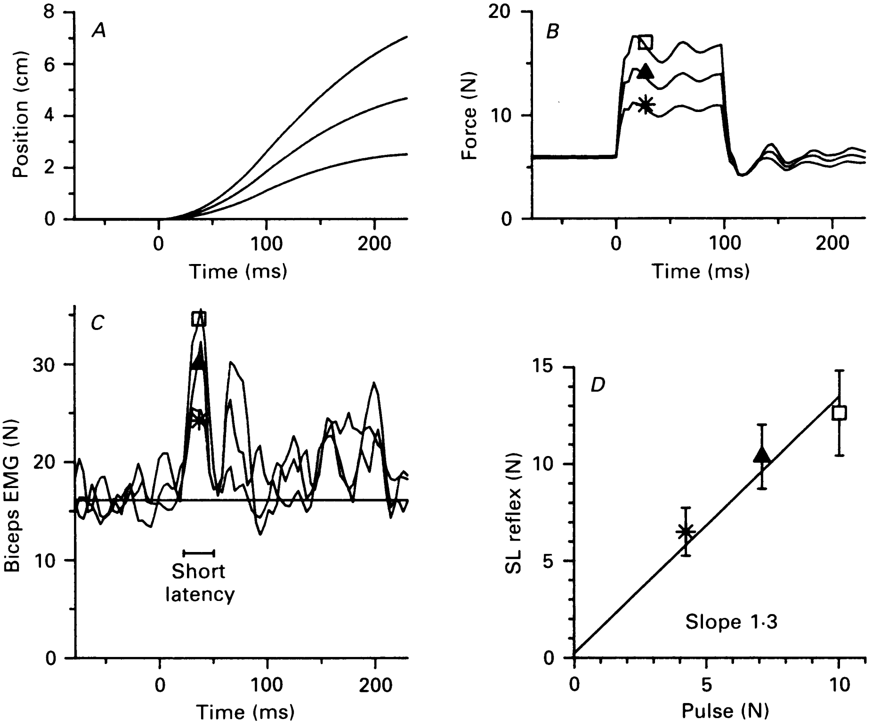

Fig. 2. Averaged data for the three amplitudes of perturbations of a typical experiment. The pre-load force was 6 N along the rail and 8 N perpendicular to the rail towards the subject. *A*, the position of the hand. *B*, the force component in the direction of the rail. *C*, averaged record of the EMG activity of m. biceps (lateral head). The EMG activity (expressed in Newtons) during the pre-load period is larger than the component of the pre-load in the direction of the rail, because the pre-load had a large component perpendicular to the rail, directed towards the subject. *D*, the mean increase of the EMG during the short-latency period in *C*, plotted against the amplitude of perturbation. The vertical bars indicate the standard error of the mean. The line is obtained by a least-squares fit to the data and the point (0, 0); the slope of the line is called the (dimensionless) reflex gain.

We realize that although we express the EMGs in Newtons, there is no fixed relation between the EMG of a muscle and the force the hand exerts. For instance, the same force can be achieved by different combinations of muscle activities (Tax, Denier van der Gon & Erkelens, 1990).

Furthermore, it is not self-evident that the relation between force and EMG is exactly the same for voluntary isometric contractions and reflex contractions. It was not possible to derive an EMG–force relation for reflex contractions because we could not separate the reflex force from the passive viscoelastic and inertial forces induced by the perturbation.

Using this method, however, we corrected for some effects of differences in the positions of the electrodes, thus reducing the inter-subject variations of the EMG recordings.

We used the following procedure to determine the gain of the short latency reflex (see Fig. 2). For each trial, the background activity was calculated as the average EMG during the 200 ms before the perturbation. The reflex activity was then calculated as the difference between the EMG averaged over the short-latency period (22–50 ms after the start of the perturbation) and the background activity. For each of the three perturbation amplitudes, the calculated reflex activities were averaged over about twenty-five trials. The reflex gain is defined as the ratio between reflex activity (expressed in Newtons) and perturbating force. To calculate the gain of the 'long-latency' reflex we used the same procedure; for this reflex component the EMG was averaged between 50 and 100 ms after the start of the perturbation.

RESULTS

The perturbations which extended the shoulder, leaving the elbow angle unchanged, elicited short-latency reflexes not only in m. pectoralis and m. biceps, but also in m. brachialis, which was not stretched by the perturbations. It was found that if m. triceps was active during the pre-load period this muscle was inhibited during the short-latency period. All subjects showed similar responses to these perturbations.

To test whether the short-latency reflex in m. brachialis depends on the direction of the perturbation, or whether it was a reaction that occurred in response to any impulse on the hand, we performed with two subjects an experiment with force pulses that flexed the shoulder, leaving the elbow angle unchanged. In these experiments, m. triceps showed a clear short-latency reflex, while the flexors (including m. brachialis) were inhibited during the short-latency period. The short-latency reflex in m. brachialis is therefore not caused by vibration or pressure induced by the perturbation.

It follows from geometry that both in the shoulder-flexion experiment and in the shoulder-extension experiments the elbow is very slightly extended. Since the sign of the reflex reverses when the shoulder movement is reversed, it is unlikely that the short-latency reflex in m. brachialis is caused by this slight elbow extension. To test the effect of slight elbow movements, we performed an additional experiment with one subject. In this experiment the rail was rotated a few degrees, so that the force pulses caused a shoulder extension accompanied by a slight elbow flexion. The rotation of the rail had very little effect on the short-latency reflex activity in m. brachialis.

We checked that the short-latency reflex in m. brachialis was not caused by cross-talk from m. biceps. By comparing the ratio of $\mathrm{EMG}_{biceps}/\mathrm{EMG}_{brachialis}$ for flexion and supination torques, we estimated the cross-talk from m. biceps to the brachialis electrodes to be certainly less than 15%. Since the reflexes in both muscles were about the same size we could rule out the possibility that a significant part of the measured reflex in m. brachialis was due to cross-talk from m. biceps. With these tests we have confirmed that the short-latency reflex we measure in our experiments in m. brachialis is a heterogenic reflex.

In all muscles the amplitude of the short-latency reflex increased with the pre-load activity of that muscle. If, due to the direction of the pre-load, a muscle was silent before the perturbation, it showed hardly any reflex activity. In Fig. 3 we have plotted the measured short-latency reflex gains for four muscles. All subjects showed roughly the same increase of the short-latency reflex gain with pre-load. Having pooled the data of all subjects, we determined the slope of the relation between reflex gain and pre-load activity. To investigate the dependence of the reflex gain on the torques about both joints, we determined the slope of the relation between reflex gain and pre-load torques (Table 1).

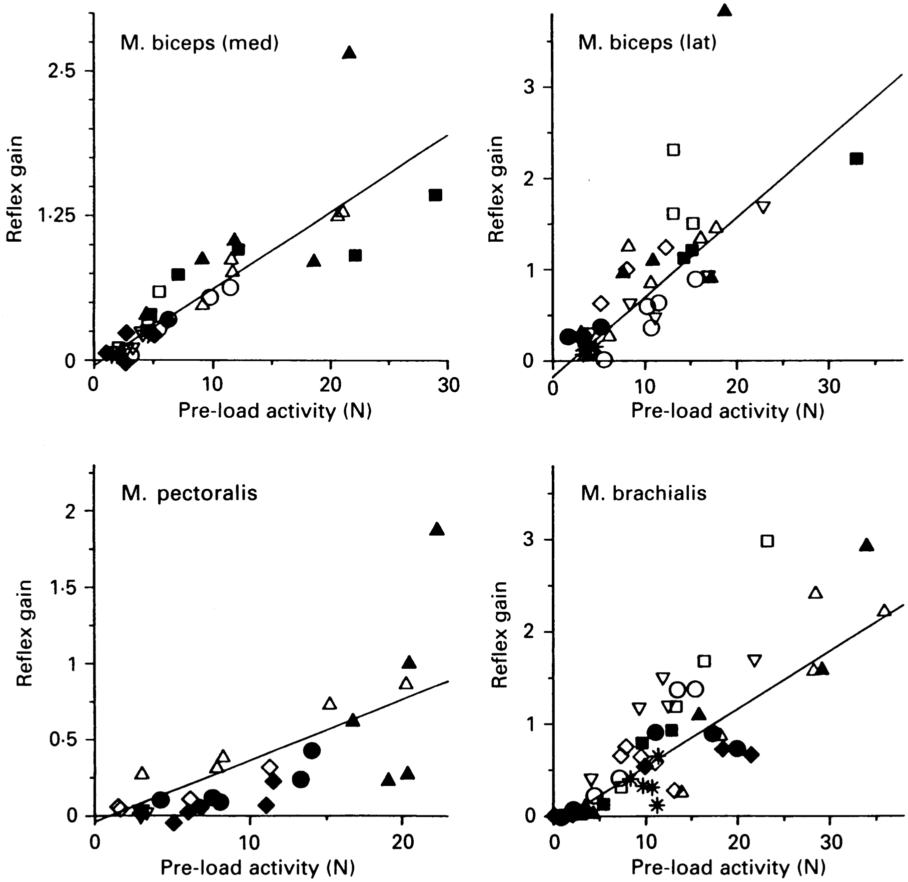

Fig. 3. For four muscles, (biceps (lateral and medial head), pectoralis major and brachialis), the gain of the short-latency reflex as a function of the pre-load activity of the muscle. Each symbol represents a different experimental session. In all four muscles (including m. brachialis, which was not stretched by the perturbation) the reflex gain increases with pre-load activity. Weighted linear regressions are used to fit the data of all the subjects.

In the short-latency period the reflex gain of all muscles increased with the pre-load torque about the joint(s) over which the muscle acts. The short-latency reflex gain of m. pectoralis major increased with its activation, and also increased with the pre-load torque about the shoulder, but was almost independent of the pre-load torque about the elbow.

The short-latency reflex gain of m. brachialis did not depend significantly on the pre-load torque about the shoulder, but clearly increased with the pre-load torque about the elbow (see Fig. 4). Because the short-latency reflex gain in m. pectoralis clearly increased with the pre-load torque about the shoulder, whereas the short-latency reflex gain of m. brachialis remained more or less unchanged, we conclude that the direction of the reflexively induced reaction force depends on the direction of the pre-load.

TABLE 1. For four muscles, the slope of a linear regression fit of the reflex gain as a function of the pre-load activity, and the slopes of a multiple linear regression fit of the reflex gain as a function of the torques about elbow and shoulder. Reflex gains of all subjects were pooled prior to the regression analysis. Values for both the short-latency reflex (22–50 ms) and the long-latency reflex (50–100 ms) are given (±S.E.M.)

	Short-latency reflex			Long-latency reflex			Number of experi-ments
Muscle	Pre-load $(10^3\,\mathrm{N})^{-1}$	Shoulder $(10^2\,\mathrm{N\,m})^{-1}$	Elbow $(10^2\,\mathrm{N\,m})^{-1}$	Pre-load $(10^3\,\mathrm{N})^{-1}$	Shoulder $(10^2\,\mathrm{N\,m})^{-1}$	Elbow $(10^2\,\mathrm{N\,m})^{-1}$	
Brachialis	62±7	3±3	30±3	37±8	15±4	14±4	50
Biceps (lateral)	87±10	16±4	24±5	44±15	23±4	8±6	41
Biceps (medial)	66±5	10±3	9±3	27±13	18±5	−1±4	40
Pectoralis major	40±5	8±3	2±3	43±12	18±5	−2±4	30

The short-latency reflex gain of m. biceps increased with the pre-load torques about both elbow and shoulder. Because the short-latency reflex in m. pectoralis major did not depend significantly on the pre-load torque about the elbow, the increase of the short-latency reflex in m. biceps and m. brachialis with the pre-load torque about the elbow is again in conflict with the hypothesis that the direction of the reflexively induced force is independent of the direction of the pre-load.

Generally, the long-latency reflexes also increased with the pre-load activity, but the correlation was far less than for the short-latency reflex. For the muscles contributing to elbow flexion, the increase of the reflex gain with the pre-load torque about the elbow was reduced during the long-latency period with respect to the short-latency period. On the other hand, the gain of the long-latency reflex in all the elbow flexors increased significantly with the pre-load torque about the shoulder, and this increase was larger than during the short-latency period. For m. pectoralis major, the reflex gain behaved in more or less the same way during both periods: the gain increased with the pre-load torque about the shoulder, but not with the pre-load torque about the elbow. The long-latency reflex gains are thus almost independent of the pre-load torque about the elbow, and all increase with the pre-load torque about the shoulder. So, in contrast to the short-latency reflex, the long-latency reflexes behave more or less according to the predictions made in the Introduction.

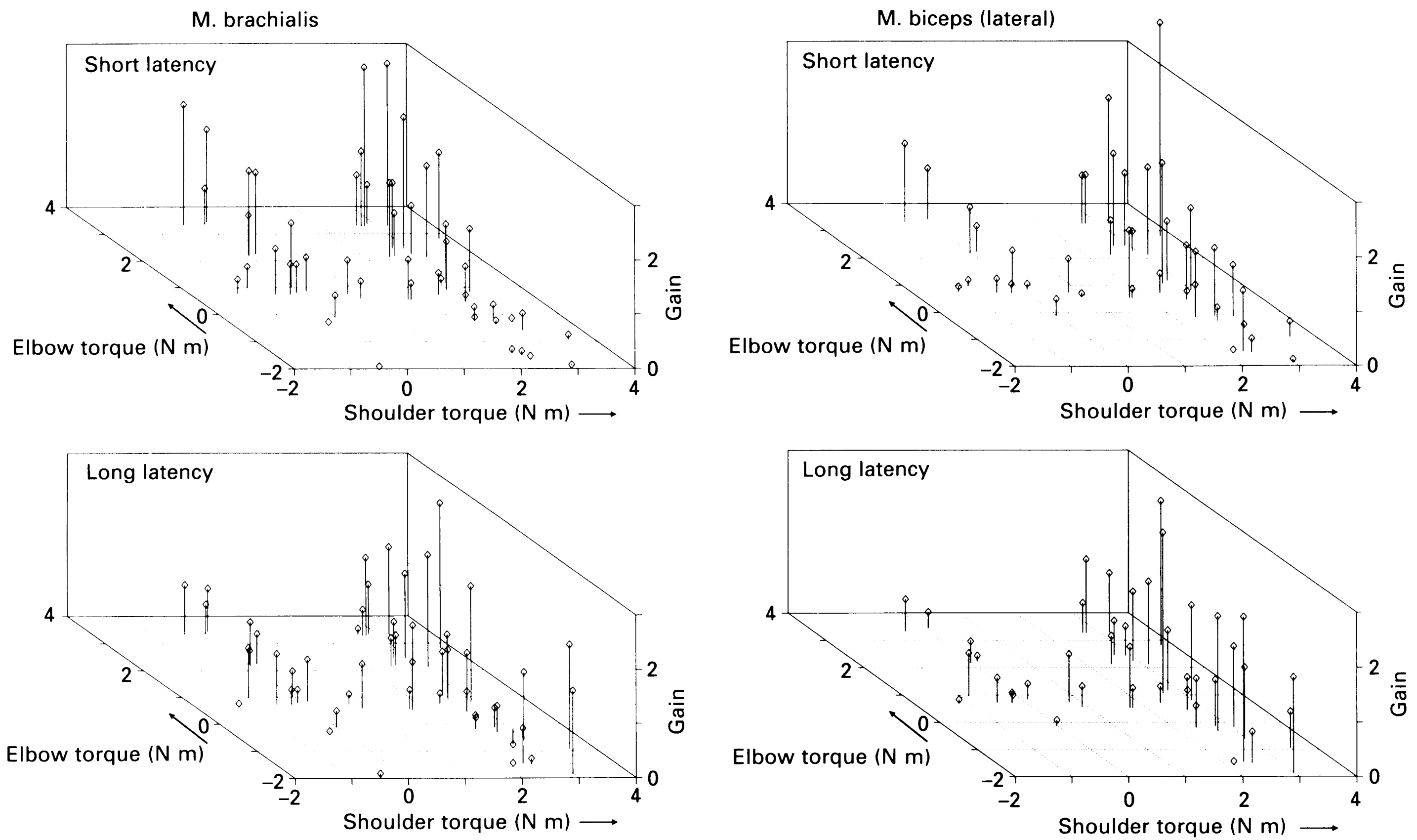

Fig. 4. For two muscles (brachialis and biceps (lateral head)), the reflex gains for both short and long-latency reflexes are plotted as a function of the pre-load torques about shoulder and elbow. For clarity, we used one symbol for all the subjects. For both muscles, compared to the short-latency reflex gains, the long-latency reflex gain is more correlated with the pre-load torque about the shoulder and less correlated with the pre-load torque about the elbow.

DISCUSSION

We have shown that the amplitude of the short-latency reflex in a muscle depends on the pre-load activity of the muscle, regardless of whether the reflex is elicited by stretch of the same muscle or by stretch of other muscles. Therefore the direction of the force induced by the short-latency reflex depends on the direction of the pre-load. The amplitude of the long-latency reflex, however, depends predominantly on the pre-load activity of the muscles that are stretched. So the direction of the force induced by this reflex depends far less on the direction of the pre-load.

Several explanations have been proposed for the increase of the short-latency reflex gain with the pre-load of the muscle: a separate (μ) input (Marsden *et al.* 1976), an effect of α–γ co-activation (Wadman *et al.* 1980), and characteristics of the motoneuron pool (Matthews, 1986). Models of the characteristics mentioned by Matthews are given by Harrison & Taylor (1981) and Capaday & Stein (1987*a*). Matthews' argument is supported by the finding by most authors that the amplitude of the H reflex also increases about linearly with the pre-load activity of the muscle (Hoffmann, 1922; Capaday & Stein, 1987*b*; but cf. Rüegg, Krauer & Drews, 1990). The increase of the reflex gain due to the characteristics of the motoneuron pool is independent of the autogenic or heterogenic source of the excitation. Therefore, this mechanism also predicts a linear increase of the heterogenic reflex gain with the pre-load activity.

We found that the short-latency reflex gain in a muscle that is not stretched (m. brachialis) is independent of the activation of the muscles that are stretched. This makes it likely that the afferent signals from the muscles that are stretched are independent of the activity of these muscles. However, since the extrafusal fibres are stiffer when activated, the stretch of the spindles will be less for an activated muscle. Thus, to retain the same output, the activation of the dynamic γ-fibres has to increase with the α-activation during isometric contractions.

In concluding that the short-latency reflex is not an adequate one, we have neglected the mechanical properties of the muscles. Houk (1976) suggested that the reflex activity is a compensation for these properties. The mechanism stiffness increases with the activity of a muscle (Joyce, Rack & Westbury, 1969). To compensate for the mechanical properties, the reflexes should have been largest in the muscles that were compliant. Because the reflexes also increase with pre-load, they do not compensate for the mechanical properties; on the contrary.

The results of this study provide an explanation for a phenomenon described by Lacquaniti & Soechting (1986*a*). They investigated changes in EMG activity, averaged over a period corresponding to 20–70 ms on our time scale, in response to perturbations of arm position. They found that the EMG responses were not related simply to the change in the length of the muscles. The EMG responses, however, did correlate very well with the change in the torque about the joint(s) over which the muscle acted. Since the change of torque about a joint is not a quantity that is directly sensed by the nervous system, and the responses were found at short latency, it seems likely that a simple mechanism is responsible for this correlation. In the experiments of Lacquaniti & Soechting (1986*a*), the pre-load force was always exerted in the same direction as, or in the opposite direction to, the perturbation.

Therefore, the muscles that were activated by this pre-load generated torques about elbow and shoulder in the same ratio as the perturbation. The ratio of the pre-load activity of the muscles correlated therefore with the ratio of the torques generated by the perturbation. Thus the correlation between the reflexes and the perturbating torques can be a manifestation of the described increase of short-latency reflex gain with pre-load activity.

Although in our experiments we found reproducible short-latency reflexes in muscles that were not stretched, other authors report that these reflexes are difficult to reproduce (Lacquaniti & Soechting, 1986*b*; Gielen *et al.* 1988). An explanation for this variability is that short-latency reflex actions can change dramatically as the subject's task changes (Evarts & Granit, 1976; Capaday & Stein, 1987*b*). For the heterogenic reflexes in the decerebrate cat, Nichols (1989) has shown that even the sign of the reflex can change. Even differences in task execution which are not observed by the experimenter can cause large deviations in motor output. Tax *et al.* (1990) showed that moving an object with a prescribed velocity against a constant load and exerting a prescribed force against a moving object are different tasks, in which even the recruitment frequency of motor units is different.

We have not paid much attention to the long-latency component of the stretch reflex. It has been shown already by Gielen *et al.* (1988) that this component resembles voluntary activation patterns used for a movement against the perturbation. In our experiments too, the long-latency reflexes were shown to be quite adequate. Since the perturbation was always in the same direction, the intention of the subject could have played an important role here.

One could ask whether the relation between the short-latency reflex and the pre-load activity depends on the instruction to the subject. Evarts & Granit (1976) showed that the short-latency reflex is not sensitive for instructions to the subject, but the short-latency reflex can become more adequate by repetition of the experiment with the same instruction. Because the intended movement (indicated by the long-latency reflex) was almost in the same direction in all our experiments, we conclude that the short-latency reflexes we studied were probably as adequate as possible.

We find it remarkable that the reflex gain in m. pectoralis is the lowest of all gains. We certainly did not expect the gain of heterogenic reflex in m. brachialis to be higher than the autogenic reflex in m. pectoralis. However, because the relation between reflex EMG and force is not known and is not necessarily the same for all muscles, we do not know whether the mechanical effect of the reflex is also the least in m. pectoralis.

We argued that the short-latency reflexes were not an adequate reaction to the perturbations in this experiment, but were more than mere mechanisms controlling muscle length. In the present experiments we have tested the adequacy of the short-latency reflex in a somewhat artificial situation. If might be, however, that the short-latency reflex is a very adequate response to perturbations during more natural tasks in which adequate responses are desirable at short latency. For fast goal-directed movements, Smeets *et al.* (1990*b*) have shown that adequate adjustments in the EMG could be observed about 35 ms after the nervous system had detected the unexpected load. This result is not in conflict with the data presented in this paper, because the perturbation was in the same direction as the movement. For perturbations in the direction of movement, the reflexes described in this paper are adequate: the direction of the adjustment must depend on the direction of movement, and thus on the activation level of the muscles prior to the perturbation.

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