Habituation and conditioning of the human long latency stretch reflex

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Summary. The effects of stretch repetition rate, prior warning stimuli and self administered stretch were examined on the size of the short and long latency components of the stretch reflex electromyographic EMG response in flexor pollicis longus and the flexor muscles of the wrist and fingers. Stretches of constant velocity and extent were given every 10 s, 5 s, 2 s, or 1 s to either the wrist or thumb during a small background contraction of the flexor muscles. The size of the long latency component of the stretch reflex (measured as the area under the averaged rectified EMG responses) declined dramatically at faster repetition rates, especially in the wrist and finger flexors. The size of the short latency component was relatively unaffected. The size of the electrically elicited H-reflex in forearm muscles also failed to habituate under the same conditions. If each individual trial of a series was examined, the long latency component of the stretch reflex EMG could be seen to decrease in size over the first three to six stretches if stretches were given every 1 s, but not if stretches were given every 10 s. When stretches were given every 5 s to either wrist or thumb, an electrical stimulus applied to the digital nerves of the opposite hand 1 s before stretch reduced the size of the long latency component of the reflex EMG response. The short latency component was unaffected. Self triggering of wrist or thumb stretch by the subject pressing the stimulator button himself with his opposite hand, also decreased the size of the long latency component of the reflex EMG response without affecting the short latency component. It is concluded that factors other than stretch size or velocity can have marked effects on the size of the long latency component of the stretch reflex. These factors must be taken into account when comparing values of reflex size obtained with different stretching techniques and in different disease states in man.

Key words: Stretch reflex – Habituation – Human

Introduction

There have been many studies on the stretch reflexes of normal subjects and neurological patients (e.g. Desmedt 1978 for references), yet little attention has been paid to conditions other than stretch amplitude and velocity which might influence reflex size. However, many other human reflexes are known to be influenced by factors other than stimulus intensity. A well-documented phenomenon is the gradual decrease in size of reflex responses to a repetitive series of identical stimuli, known as habituation. For example, the size of the electrically evoked blink reflex (Kugelberg 1952; Sanes and Ison 1983) or of the cutaneous flexor reflex after electrical stimulation of the foot (Shahani and Young 1971), depends on the rate and regularity at which stimuli are given. The presence of a prior warning stimulus or self-triggering the stimulator also affects the size of some reflex responses. A prior auditory, visual or somaesthetic stimulus can reduce the amplitude of the late (R2) component of the blink reflex (Boulu et al. 1981). Self-administration of stimuli (by pressing the stimulator button oneself) also depresses the size of blink and cutaneous flexor reflex responses (Young 1973).

Factors such as these have not been considered as possible influences on the size of the mechanically-

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evoked stretch reflex in muscles of the arm. Nashner (1976) showed that the functional stretch reflex evoked in calf muscles of a freely standing subject either diminished of facilitated progressively over consecutive trials depending upon whether the reflex was appropriate to reduce body sway. However, this reflex may not be directly comparable to the stretch reflex evoked by passive stretch in muscles of the arm or leg. It was present in only 5 out of 12 subjects, and appeared at an unusually long latency (120 ms). The only other investigations on adaptation in human stretch reflex pathways have used electrical stimulation to produce H-reflexes in the muscles under test. Habituation of the H-reflex has been studied in some detail. In active muscles, the H-reflex in triceps surae does not habituate at repetition intervals as short as 1 s, but in relaxed muscles the H-reflex is known to habituate at repetition intervals up to 5 s (Hoehler et al. 1981). The H-reflex is mediated largely monosynaptically via muscle spindle Ia afferents, a pathway which is thought to be shared by the mechanically elicited tendon jerk. It would, therefore, be surprising if the tendon jerk did not habituate in the same way.

The stretch reflex of muscles in the upper limb consists of more than the tendon jerk. In the EMG record there are two distinct components, a short latency spinal event (analogous to the tendon jerk) followed by a later, long-latency, reflex event, the origin of which still is debated (see Marsden et al. 1983). In this paper we have examined the effect of presentation rate on the short and long latency components of the mechanically evoked stretch reflex of flexor pollicis longus and of the flexor muscles of the wrist and fingers. In addition, we have examined the effect of prior warning stimuli and of self triggered stretches on the size of the two components of the reflex. Part of these data have been published previously in abstract form (Berardelli et al. 1985).

Methods

Stretch reflexes were elicited in the flexor pollicis longus and the wrist and finger flexor muscles of the forearm in six normal subjects aged 22–35 years. For the flexor pollicis longus, subjects sat with their semi-pronated forearm supported before them on a table, and with the thumb pad resting on the lever arm of a small torque motor (Printed Motors type G9M4H). The interphalangeal joint of the thumb was aligned with the axis of rotation of the motor shaft and the proximal phalanx was clamped so that movement was limited to the distal phalanx. The starting position of the thumb was at approximately 30° flexion at the interphalangeal joint. For the wrist and finger flexor muscles, the semi-pronated forearm rested on a platform above a torque motor (Printed Motors type G12M). The fingers were encased in a rigid

splint attached to the motor and the wrist was aligned with the motor shaft. The forearm was then clamped securely to allow movement only at the wrist joint. The starting position was approximately 30° flexion at the wrist joint.
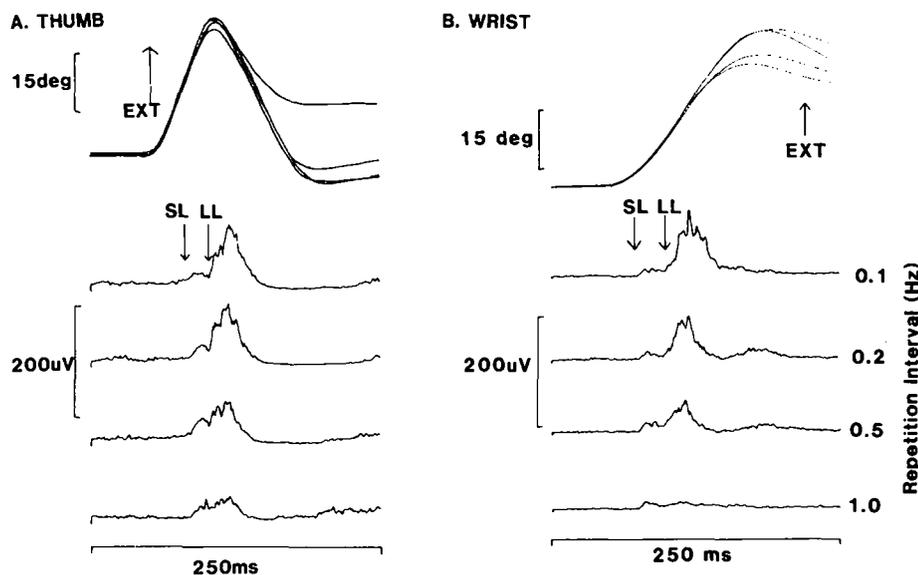
The parameters of stretch were chosen so as to produce submaximal stretch reflexes in the two muscles studied. For flexor pollicis longus, subjects held their thumb in a constant position with reference to an oscilloscope display before them against a steady standing torque of 0.06 Nm. Stretches were given by increasing the torque to 0.20 Nm for 50 ms. At the wrist, the standing torque was 0.16 Nm, rising to 1.1 Nm for 200 ms. Stretches either were given regularly every 10 s, 5 s, 2 s or 1 s, in batches of 32 trials, or were given irregularly with one of the four intervals between stretches chosen at random. With regular presentation, the subjects knew the timing of muscle stretch, whereas with irregular presentation this could not be forecast. Subjects were instructed not to react to the stretch in any way (i.e., by opposing or assisting the motor), but to maintain a constant level of muscle activation throughout the experiment. Joint angular position (from an infinite resolution Bourns 2″ diameter servopotentiometer mounted on the motor shaft), joint velocity (by analogue differentiation of the position signal), and rectified surface EMG (from Ag/AgCl electrodes placed over the muscles) were recorded. The EMG was amplified by Devices 3120 and 3160 amplifiers with bandpass filters set at 80 Hz and 2.5 kHz (3 dB points). All data was collected by a PDP12 computer with a sampling rate of 1 kHz per channel and stored on floppy discs using programmes devised by Mr. H.B. Morton.

A second series of experiments was performed on six different subjects aged from 30–37 years. Stretches were given, as above, to the thumb or wrist at 5 s intervals. In half the trials, at random, a 200 ms train of electrical stimuli (50 Hz, 300 µs; Disa constant current stimulator type 15 E07) at twice sensory threshold was given via ring electrodes to the contralateral index finger 1 s before stretch onset. Subjects were instructed not to respond in any way to the stimulation. 32 trials were averaged with and without the preceding stimulus.
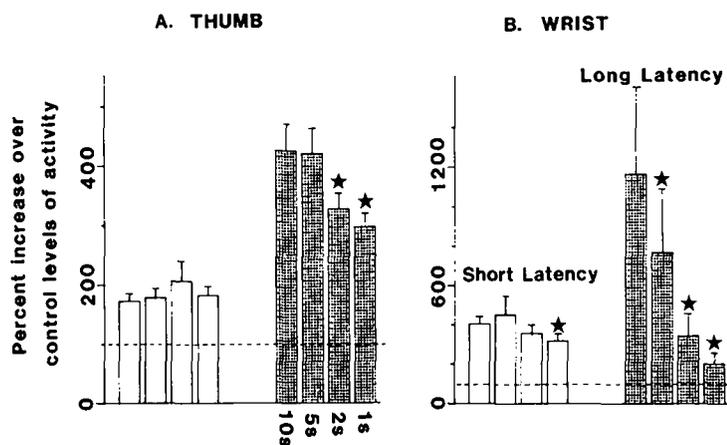
A final group of experiments was made on five further subjects aged 30–37 years. Stretches were given to the thumb or wrist automatically every 5 s, or were triggered individually by the subject himself pressing a button with the other hand at approximately 5 s intervals. Two groups of sixteen consecutive trials of each type were averaged and compared.

The reflexes were measured by visual inspection on the computer display of averaged records of full-wave rectified EMG activity. The end of the short latency and beginning of the long latency reflex was determined by an abrupt increase in the averaged surface rectified EMG at a latency of between 45 and 50 ms for both muscles studied. First, the duration of the spinal and long latency components of the EMG responses were estimated. Then, the size of the reflex at every repetition rate was taken as the integral of the rectified EMG activity measured by the computer within the same interval. Finally, this size was expressed as a percentage of control levels of EMG activity extrapolated from the first 50 ms of the sweep, before stretch was delivered.

H-reflexes were evoked in wrist and finger flexor muscles by stimulating the median nerve in the cubital fossa with single submotor threshold electrical pulses of 1 ms duration (for details see Day et al. 1984). Stimuli were given as for stretch in batches of 32 at intervals of 10, 5, 2, and 1 s. This procedure was performed with the subject at rest and whilst holding the wrist at a constant position against a steady extending torque of 0.16 Nm which was supplied by the torque motor. The amplitude of each H-reflex was measured peak to peak. The size of the electrical stimulus was adjusted so that control reflex sizes were approximately the same when the subject was activating the flexor muscles as when relaxed.

A. THUMB

15deg

EXT

SL LL

200uV

250ms

B. WRIST

15 deg

EXT

SL LL

0.1

0.2

0.5

1.0

Repetition Interval (Hz)

250 ms

Fig. 1A and B. Average (of 32) changes in joint angle (superimposed upper records) and rectified EMG responses (four lower records) in response to stretch of flexor pollicis longus (A, Thumb) and flexor muscles in the forearm (B, Wrist) given at different repetition intervals in one subject. The EMG responses in both muscle groups consist of a short (SL) and long (LL) latency component with onset latencies indicated by the vertical arrows. As the repetition interval is decreased, the size of the LL component decreases, but the SL component remains approximately the same size. The mechanical consequences of the change in EMG responses can be seen in the position records. Those records showing the most rapid return to the starting position belong to EMG records which have the largest stretch reflex responses

A. THUMB

Percent increase over control levels of activity

400

200

0

10s 5s 2s 1s

B. WRIST

Long Latency

1200

600

Short Latency

0

Fig. 2A and B. Average data (with 1 S. E.) from six subjects showing the change in size of short latency (open bars) and long latency (hatched bars) components of the stretch reflex when stretches are given at four different intervals (10 s, 5 s, 2 s, and 1 s. A shows results from flexor pollicis longus, B from flexor muscles in the forearm. the size of the two components of the e.m.g. response is expressed as a percentage of the background level of EMG activity (= 100%, dotted line). When the interstretch interval was small, the long latency components in both thumb and wrist were smaller than when stretches were given every 10 s. (* = $p < 0.05$ for paired comparisons in each subject with the 10 s interval).

Results

When stretches were given at regular intervals to either the thumb or to the wrist, and the EMG responses were averaged over 32 trials, the size of the stretch reflex was highly dependent on the rate at which the stretches were presented. For thumb stretches, the effect was limited to the long latency component of the reflex in flexor pollicis longus (Fig. 1a). Its size decreased to about 60% of its value at 1 s intervals compared with the size at 10 s intervals (Fig. 2a). Whether thumb stretches were given at 10 s intervals of 1 s intervals, the size of the short latency spinal component remained unchanged. The initial parameters of stretch (the position 50 ms after stretch onset, and peak velocity of stretch) did

not change with repetition rate (Table 1). For wrist stretches, there was a small decrease in the size of the spinal component of the reflex when stretches at 10 s and 1 s intervals were compared, but not at any other intervals (Fig. 1b and 2b). However, there was a striking decline in the size of the long latency stretch reflex at all repetition rates below 10 s intervals. As with the thumb, the initial mechanical parameters of wrist stretch did not change with repetition rate (Table 1).

The duration of the long latency stretch reflex was measured at different presentation frequencies. It remained constant in the flexor pollicis longus, but decreased considerably in the wrist and finger flexor muscles as the repetition rate increased. When stretches were given every 1 s, the duration

Table 1. Mechanical parameters of stretch at different repetition intervals in six subjects

		Repetition interval			
		10 s	5 s	2 s	1 s
Thumb	Position (deg)	27 ± 4	29 ± 4	30 ± 4	27 ± 4
	Max. vely. (deg/s)	682 ± 81	743 ± 90	770 ± 104	678 ± 62
Wrist	Position (deg)	9 ± 1	9 ± 1	9 ± 1	10 ± 1
	Max. vely. (degs/s)	321 ± 37	312 ± 39	295 ± 28	345 ± 41

Change in position of the thumb or wrist was measured 50 ms after stretch onset. Figures are mean $\pm$ 1 S.E. Repetition interval has no effect ($p > 0.05$) on either position or velocity measurements

H REFLEXES
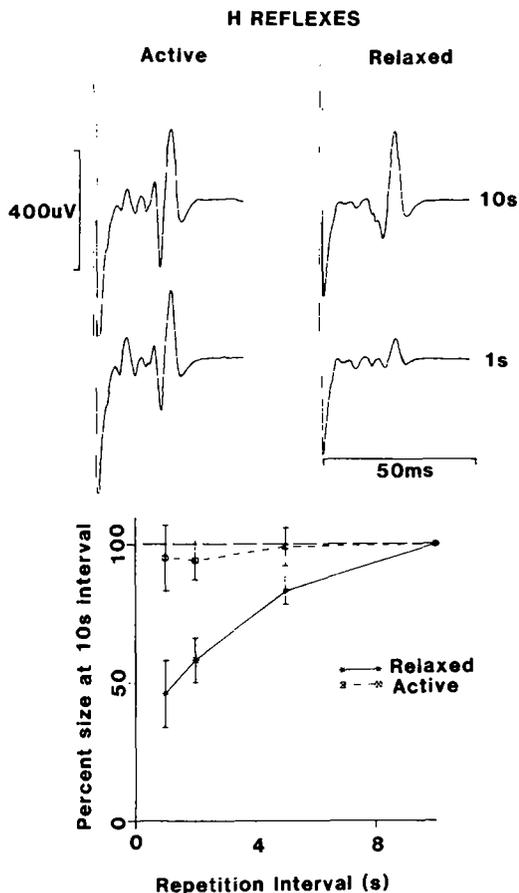
Active   Relaxed

Fig. 3. Comparison of habituation of the H-reflex in the flexor muscles of the forearm when subjects are active and relaxed. Upper panel: raw data from one subject. Traces show the average of 16 H-reflexes elicited either every 10 s (top records) or every 1 s (bottom records). Those on the left were elicited whilst the subject maintained a small background flexor contraction of the wrist against an isotonic opposing torque of 0.16 Nm, those on the right were elicited at rest. With the subject relaxed, the H-reflex becomes much smaller when evoked every 1 s compared with every 10 s. Lower panel: average data ($\pm$ 1 SE) from six subjects. The size of the H-reflex in each subject was expressed as a percentage of its size when stimuli were given every 10 s
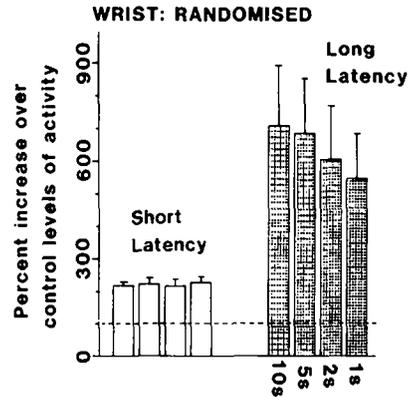
Fig. 4. Average ($\pm$ 1 S.E.) data from four subjects showing how the size of the short and long latency components of the stretch reflex in the wrist changes with interstretch interval when the interval is randomised from trial to trial. Reflex size is expressed as a percentage of background EMG levels ($= 100\%$, dotted line). Although there is a trend for the long latency component to be smaller when the interstretch interval is shorter, this is not as pronounced as when the intervals were not randomised (see. Fig. 2). There was no difference ($p > 0.05$) between each interval and the size at 10 s

(22 ± 3 ms; mean $\pm$ 1 SE) was less than half that seen when stretches were given every 10 s (46 ± 3 ms).

We confirmed that with the subject at rest H-reflexes elicited in wrist and finger flexor muscles habituated at interstimulus intervals of 1 to 10 s (Fig. 3). However, stretch reflexes were obtained with the muscles activated voluntarily to maintain a constant position against a background force. When H-reflexes were elicited with the subject exerting a similar background contraction the H-reflex failed to habituate (Fig. 3).

The decline in the size of the long latency reflex with increasing rates of muscle stretch was not seen as clearly when the presentation rate was varied from trial to trial, rather than remaining constant at a given interval over many trials. The results from four subjects in whom stretch intervals of 10 s, 5 s, 2 s and 1 s were intermixed at random, and the EMG responses averaged over 32 trials, are shown for the wrist and finger flexor muscles in Fig. 4. The size of the spinal component of the reflex was unaffected by presentation rate. However, the long latency component tended to decrease in size as the stretch interval decreased, although the effect was considerably less than that seen with regular presentation.

In order to investigate the reason for the difference between regular and irregular presentation rates, each single trial of a sequence of regular stretches was investigated. When this was done, the long latency stretch reflex could be seen to habituate

F.C.R.

1s Interval   10s Interval
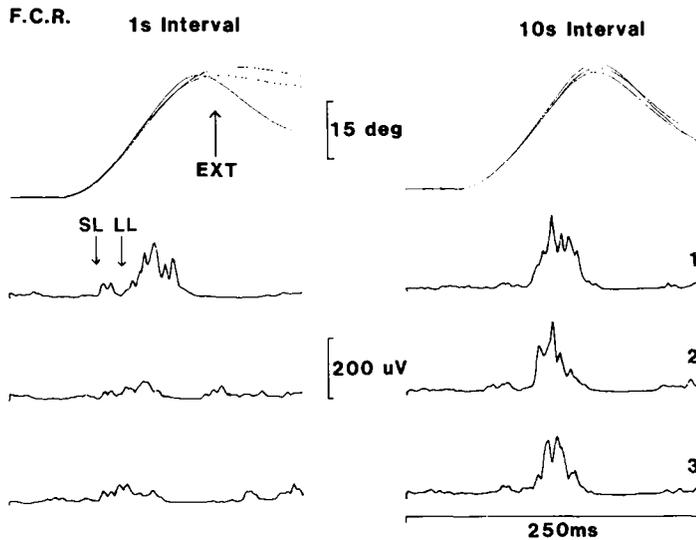
Fig. 5. Habituation of the stretch reflex in the flexor muscles of the forearm over the first 9 stretches of a series. Traces are from one subject. Each is the average of three consecutive trials when stretches were given every 1 s (left) and every 10 s (right). Averages of the first, second and third set of 3 trials are shown separately for the EMG response (below: 1, 2, 3), and superimposed for the wrist position records (above). Onset of the short latency (SL) and long latency (LL) components of the reflex EMG response are indicated by vertical arrows. On the left, the position trace which returns most rapidly towards the starting position is the average of the first 3 stretches. The EMG response (1) to these initial stretches was much larger than that to the subsequent (2, 3) sets of stretch when stretches were given every 1 s. There was little difference in size when stretches were given every 10 s
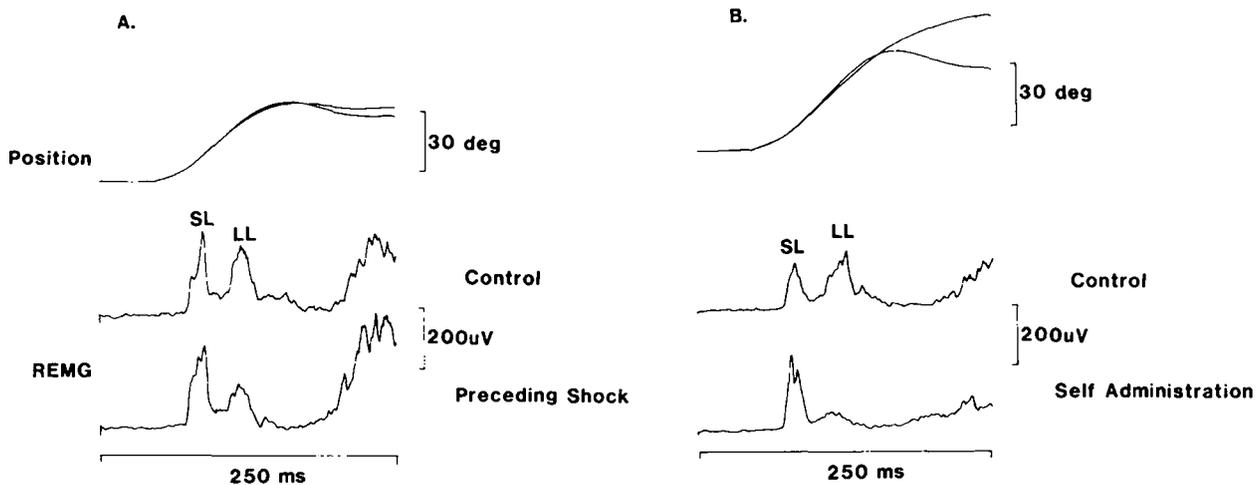
Fig. 6. A Effect of giving a single preceding electrical stimulus at twice sensory threshold to the contralateral finger on the stretch reflex recorded in the flexor muscles of the forearm. B Effect of self administering the stretch on the size of the reflex. Upper traces are superimposed position records of wrist joint angle. Lower two traces are average (of 32) EMG responses in one subject. Short (SL) and long (LL) latency components of the e.m.g. response are indicated. The position traces which show the most rapid return towards the starting position correspond with the EMG records with the largest LL reflex response. The size of the SL component is unaffected by a preceding shock, or by self-administration whereas the LL component is greatly reduced

over the initial trials if given at high repetition rates. This is illustrated in Fig. 5 for the wrist and finger flexors. Because the size of the reflex is difficult to estimate in single trials, sequential averages of consecutive groups of three stretches are shown. When given every 10 s, there was no decline in size of the long latency reflex. In contrast, if stretches were given every 1 s, the reflex habituated rapidly between the first two groups of averages.

Finally, two other factors were tested for their effect on stretch reflex size. The first was the presence of a warning stimulation given 1 s prior to

stretch onset. Stretches were given every 5 s to the thumb or wrist and were preceded in random trials by a short (200 ms, 50 Hz) train of electrical stimuli given 1 s earlier to the forefinger of the opposite hand. The size of the long-latency component of the reflex in both the thumb and wrist flexors was smaller in trials in which the electrical stimulus was given, although the spinal component was unaffected (Figs. 6A and 7). In the second experiment, subjects triggered the stretch themselves about every 5 s by pressing a button with the contralateral hand. Again, the size of the long latency response was much
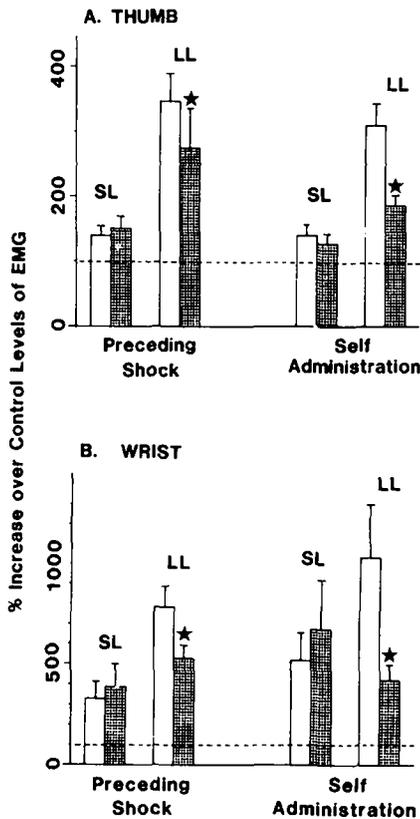
Fig. 7A and B. Average (± 1 S.E.) effect of preceding electrical shocks or self-administration on the size of the stretch reflex in 6 subjects. A results from thumb stretch; B results from wrist stretch. Short (SL) and long (LL) latency components of the reflex have been analysed separately. Size of response expressed as a percentage of background levels of EMG activity (= 100%, dotted line). Control values are shown by open bars, hatched bars show the effect of preceding shock or self administration. Stars indicate differences ($p < 0.05$) between open and hatched bars when paired data from each subject was analysed

reduced compared with the stretches given automatically every 5 s. The spinal component was unaffected (Figs. 6B and 7).

Discussion

The present results show that in addition to the known effects of stretch size and velocity, there are at least three other conditions which can have substantial effects on the size of the human mechanically evoked stretch reflex. The reflex is smaller when stretches are given more frequently, or when they are preceded by an electrical stimulus to the other hand, or when the subject self-triggers the stretches. All these effects are much more pronounced on the long-latency than on the spinal component of the response.

The change in the size of the reflex cannot be explained by a change in the voluntary intent of the subjects to respond to the stimuli. Voluntary reaction to stretch can indeed affect the size of the long-latency reflex (see, for example, Rothwell et al. 1980). However, changes in voluntary intent always are reflected in the later parts of the EMG response. For example, the intention to react to stretch increases the long-latency stretch reflex, but also is accompanied by a large, late voluntary response in the EMG record. Since the later voluntary parts of the EMG (more than 100 ms after the stretch) always were the same in our subjects, we assume that changes in voluntary intent cannot have played any part in the phenomena reported here.

This differential effect on the short and long-latency components of the stretch reflex is compatible with the idea that they are mediated by two different pathways. A number of possible routes have been postulated. Whilst most authors agree that the short-latency stretch reflex is a spinal (partly monosynaptic) event from muscle spindle Ia afferents, the mechanism of the long-latency stretch reflex is more controversial. The latter might involve a pathway separate from the classical monosynaptic IA reflex arc; possibilities that have been suggested include a transcortical route (Marsden et al. 1976; Lee and Tatton 1975), a polysynaptic spinal route (Hultborn and Wigstrom 1980), or a spinal reflex evoked by activity in muscle spindle group II afferent fibres (Matthews 1984). Although the present results do not exclude any of these hypotheses, they are relevant to another suggestion put forward by Hagbarth et al. (1981). They suggested that the long latency component is produced by repetitive Ia spindle discharge. If this were so, reduction in the size of the long latency stretch reflex with preservation of the short latency response could only occur if the frequency of stretching, or the presence of a prior warning stimulus, or self-triggering of the stretch all affected the size of the second and subsequent spindle discharges whilst leaving the initial burst unchanged. Whether this happens is not known but there are no human data to date which favour this possibility.

Although the decrease in size of the long-latency reflex with increasing frequency of stretch was striking, it is not clear what mechanism might be responsible. There are three possible sites in the stretch reflex arc at which habituation can occur: alpha-motoneurones of the efferent pathway, or central neurones within the arc (including presynaptic effects) or at the level of the sensory receptors. Alpha-motoneurones are unlikely to be the site of habituation in view of the relatively long inter-

stimulus intervals used in this study. Effects from after hyperpolarisation and Renshaw cells would be complete within 1 s. In addition, habituation of alpha-motoneurones would not explain the difference in behaviour of the short and long-latency components of the stretch reflex since they share a common motoneurone pool (Calancie and Bawa 1984).

The sensory receptors which provide the majority of the afferent input for the stretch reflex are the muscle spindles. There have been no experiments on man which have examined the effect of stretch repetition rate on muscle spindle discharge. To explain the present results, spindle discharge would have to be smaller with faster repetition rates. Since the short-latency component showed little or no habituation over the inter-stimulus intervals studied, it seems unlikely that the initial spindle discharge (at least that in Ia afferents) could be influenced appreciably by this mechanism. The behaviour of the H-reflex support this view. As for the leg (Hoehler et al. 1981), the H-reflexes in the wrist and finger flexor muscles only habituated when evoked in relaxed muscles and failed to habituate when evoked in active muscles. Thus, during a voluntary contraction both the short-latency stretch reflex and the H-reflex did not change in size over the range of interstimulus intervals studied. The Ia afferent volley responsible for the H-reflex was constant for all repetition intervals since it was induced by an electrical stimulus of constant intensity. It is likely, therefore, that the Ia afferent volley responsible for the short-latency stretch reflex remained constant also.

We cannot exclude the possibility that rapid repetition of stretches leads to reduced secondary afferent input but again, there is no data from human microneurographic recordings to support this view. We would favour the idea that habituation of the long latency component was produced by adaptation in central neuronal pathways. This includes neurones in supraspinal as well as spinal structures. If habituation occurs at the central neuronal level, then it is possible that attenuation of the reflex in the other two experiments also is produced by action on the same neuronal pool, although it is not possible to say precisely how this might occur.

The importance of these results lies in their application to studies of stretch reflex size and function. For example, it may not be suprising to find that stretch reflexes produced by frequent sinusoidal stretch or by pseudo-random binary sequences (PRBS) of stretch are different in size from those produced by ramp stretches given at infrequent intervals (Brown et al. 1982; Johnson et al. 1981; Soechting et al. 1981). Brown et al. (1982) applied

sinusoidal stretches to the thumb and concluded that the stretch reflex has too small a gain to function as a very effective error-controlled position servo-mechanism. Johnson et al. (1981) using the technique of applying PRBS displacements to the elbow joint found that the short latency spinal reflex was unexpectedly dominant. However, using infrequent ramp stretches we have found that the long latency reflex can provide very effective compensation (Marsden et al. 1983).

Similarly, it is necessary to consider the effect of stretch frequency when comparing stretch reflex size in different disease states in man (e.g. Tatton et al. 1984; Noth et al. 1983; Berardelli et al. 1983). Habituation of reflexes is affected in some neurological conditions. The cutaneous reflexes of patients with Parkinson's disease do not habituate as rapidly as normal while the reflexes of patients with Huntington's disease habituate faster than normal (Penders and Delwaide 1971; Ferguson et al. 1978; Kimura 1973; Caraceni et al. 1976). If the habituation of long latency stretch reflexes is affected in the same way, then it may be that if stretches are given with short interstimulus intervals, the size of the long latency component would be overestimated in patients with Parkinson's disease and underestimated in Huntington's chorea. Stretch repetition rate could be a crucial factor in the comparison of results. Similarly, if a subject knows when stretches are going to occur, for example by triggering stretch at the onset of a movement, or by giving stretches at a specific time after a cutaneous stimulus, the size of the reflex is likely to be smaller than if the stretch was unexpected.

The consequences of long latency stretch reflex adaptation are of interest. In forearm and hand muscles, the long-latency response is much larger than the earlier spinal event, and can provide considerable mechanical compensation for external disturbances (Marsden et al. 1983). During regular repeated disturbances the amount of compensation might decline. It may be that such conditions are best dealt with by a change in voluntary motor strategy rather than by attempts to compensate for each single perturbation. The reflex system would operate best when *unexpected* obstacles are encountered in a voluntary movement for the first time. Stretch reflex changes of the short seen in the present experiments, or something like them, must explain why skiiers and jockeys keep their bottoms still, while the ground or horse moves continuously beneath them.

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