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INTERACTION BETWEEN PRE-ACTIVITY AND STRETCH REFLEX IN HUMAN TRICEPS BRACHII DURING LANDING FROM FORWARD FALLS

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SUMMARY

1. Electromyographic (e.m.g.) profiles of proximal arm muscles were studied in human subjects falling forward onto a platform.
2. The stretching of the triceps lasted 200–300 msec for deep falls, and immediately after impact angular velocities of the elbow joint up to 1000° sec^{-1} were reached.
3. For angles of fall between 50 and 90°, more than half of the subjects exhibited marked short-latency e.m.g. responses of the triceps brachii. Such responses began 20–30 msec after touchdown, arising from a more or less plateau-like activity which started about 130 msec before impact. In some cases distinct later responses were found, the second peak having a latency of 60–80 msec after touchdown.
4. The early e.m.g. response even appeared when the subject was blindfolded and when the depth of the fall was randomly varied.
5. It is concluded that both the pre-existing activity and the spinal stretch reflex contribute significantly to the over-all activity of the triceps during stretch after impact.

INTRODUCTION

The inability of the spinal stretch reflex to contribute significantly to the force exerted by the biceps brachii after load changes (Hammond, Merton & Sutton, 1956) has led to the widely accepted view that in man the spinal stretch reflex has forfeited its importance in favour of long-loop stretch reflexes. The visco-elastic properties of a pre-activated muscle are thought to be adequate for the quick compensation of external load changes (Grillner, 1972; Melvill Jones & Watt, 1971*a*). In line with this idea was the absence of early stretch responses in the e.m.g. during tracking movements of the human thumb (Marsden, Merton & Morton, 1972, 1976*a*) and after landing from unexpected falls in man (Melvill Jones & Watt, 1971*b*). However, in the work of Hammond *et al.* (1956) only a small proportion of the range of stretch velocities which can naturally occur was covered, and even at these relatively low velocities a clear increase in the size of the spinal stretch reflex with the speed of

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stretch was observed (Hammond, 1960). The latter has been confirmed by a quantitative e.m.g. study of Gottlieb & Agarwal (1979) showing a positive correlation between the size of spinal stretch response and the velocity of stretch for the triceps surae in man. Other studies have disclosed pronounced short-latency e.m.g. responses to fast stretches of proximal limb muscles during free falls in cats (Prochazka, Schofield, Westermann & Ziccone, 1977) and during voluntary contractions of proximal arm muscles in man (Dufresne, Gurfinkel, Soechting & Terzuolo, 1978). Early e.m.g. responses appeared even during relatively slow tracking movements executed by muscles of the shoulder girdle (Marsden, Merton & Morton, 1976*b*), and in response to ramp stretches of the monkey's jaw closing muscle (Goodwin, Hoffman & Luschei, 1978).

We addressed ourselves to an investigation of e.m.g. patterns in proximal arm muscles during a stereotyped motor task in which stretch velocities of the investigated muscle were higher than in comparable studies published so far. These conditions were attained by having subjects who fell forward with outstretched arms and subsequently landed on both hands. The sudden increase in load after ground contact stretched the triceps brachii at a rate up to 10 times faster than that achieved in the experiments on biceps brachii of Hammond *et al.* (1956). It is shown that the rapid stretch of the pre-activated muscle is able to induce pronounced early e.m.g. responses in the majority of the analysed e.m.g. patterns. Early stretch reflexes of the triceps surae during running have been described in another paper (Dietz, Schmidtbleicher & Noth, 1979).

METHODS

The experiments were carried out on twenty-seven healthy subjects aged between 20 and 35 years, six of them being studied several times. The majority were athletic students. The subjects self-initiated forward falls with bodies straight and arms nearly extended. They landed with both hands on a platform of variable height (see below). The *normal experimental series* consisted of visually controlled falls which were repeated 10–40 times at a particular platform position, followed by a resting period of 5–10 min. With three subjects sixty falls were analysed at the same platform position in order to check the reproducibility of the responses. With four subjects a *pseudo-random series* of falls was performed. After a series carried out under visual control, the subjects were blindfolded and acoustic control was excluded by headphone noise. The test series consisted of ten to fifteen falls for each of four randomly varied depths of fall (50–80°). After each fall the subject was turned several times and moved around in order to disturb the spatial orientation and to exclude any clues concerning the next platform block (see below) at which he was going to be tested.

E.m.g. recording

Bipolar surface electrodes were glued to the skin over the belly of the muscle to be studied (triceps brachii, forearm flexors and extensors). In most cases, the e.m.g. of the triceps brachii was recorded simultaneously on both sides. The electrodes were connected to a 4-channel telemetric transmitter carried on the subject's back. The e.m.g. signals were stored on a 4-channel tape recorder (Tandberg) for off-line analysis. The angle of the elbow joint was monitored either by a goniometer firmly tied to the upper arm and the forearm or by cinematography (60 frames/sec).

Care was taken throughout the recording session and especially at the beginning of an experiment to detect mechanical artifacts picked up by the surface electrodes. This was done by rapidly shaking the arms of the subject and by manipulating the skin around the electrodes. Renewing the fit of the electrodes usually abolished artifacts detected in this way. Nevertheless, on a few occasions suspicious peaks were found in the averaged e.m.g. profiles. These peaks appeared simultaneously with the steep increase in force after touchdown and were of short duration (5–10 msec). When this happened, all records picked up by the improper electrode were rejected.

'Cross-talk'

Surprisingly, whenever records of the biceps brachii were taken, they were small-scale versions of the ipsilateral triceps brachii activity, exhibiting the pre-activity and the early peaks. This was due to electrotonic 'cross-talk' between the activity of the triceps brachii and the surface electrodes over the belly of the biceps brachii, as was ascertained by comparing the surface e.m.g. with the activity recorded by a concentric needle electrode in the same muscle. During contraction of the biceps brachii, the activity recorded with the surface electrode was much smaller than with the needle electrode – which of course was to be expected. But during the contraction of the triceps brachii, when almost no biceps brachii activity was monitored by the needle electrode, a fair amount of activity was picked up by the biceps surface electrodes. This impeded an investigation of the biceps brachii activity during falls. 'Cross-talk' from biceps to triceps did not affect our results because of the negligible biceps activity in this particular motor task.

'Cross-talk' between the flexor and extensor muscles of the forearm was also found, but on a smaller scale. This did not seriously affect the response patterns, however, because both muscle groups were simultaneously activated during the fall so that the strong genuine activity clearly overrode the artificial shunt activity.

Platform

At an earlier stage of the experimental work (thirteen subjects) a wooden landing platform was used, which was fortified by a metal frame and was supported at one edge by a vertical stand. The height of the support could be adjusted in order to attain different platform angles. Standard falling angles between vertical and platform level were 50, 60, 70 and 80°. The compliance of the centre of the platform was of the order of 7 mm/kN. A strain gauge was mounted on the back of the platform and was used to indicate the moment of impact.

In later experiments (fourteen subjects) an improved landing support was used: two smaller metal platforms (each 0·4 m × 0·4 m) measured the moment of platform contact and the exerted force separately for each arm. Each of the smaller platforms was equipped at all four corners and in the middle with piezo-electric force transducers, which in turn were mounted on concrete blocks. The outputs of the five transducers were summed to give the total force acting perpendicularly on each small platform. The over-all compliance of the centre of each of the small platforms (improved type) was of the order of 1·5 μm/kN, with a natural frequency of 250 Hz. The smaller platforms were movable. *Four blocks* of different heights served for support. They were built with oblique upper surfaces in order to ensure that the force of the body during landing acted perpendicularly on each small platform. In addition to the standard falling angles listed above, falls of 90° could be performed with the smaller platform mounted on a concrete floor (for illustration see inset of Fig. 1).

Data processing

Off-line, the e.m.g. was full-wave rectified and fed into an averaging computer (Nicolet, model 1072). The over-all frequency response of the processed e.m.g. was flat around 150 Hz with corner frequencies (−3 dB) at 40 and 400 Hz, respectively. The force and goniometer signals were also averaged. The frequency characteristics of the mechanical signals were flat from d.c. to 1 kHz. Initially, the averager was triggered by the strain gauge signal of the platform. In later experiments it was triggered by the force signals from the transducers of the small platform, or by the goniometer signals, with the advantage that the e.m.g. of the left and right arm could be triggered separately.

RESULTS

Early e.m.g. responses of the triceps brachii during falls with visual control

Of seventy averaged e.m.g. records taken from the left or right triceps brachii of twenty-seven subjects, two-thirds revealed clear short-latency responses (delay after touchdown 20–30 msec) at all platform positions tested. A typical example is presented in Fig. 1 together with the raw e.m.g. of the left triceps brachii of a right-handed trained subject for 90° falls. The raw e.m.g. increased about 100 msec before ground contact, when a period of about 1 sec had elapsed after the beginning of the self-initiated fall (compare Fig. 5), and it reached its maximum shortly after ground contact. The averaged e.m.g. (*C*) shows that a drop in activity occurred just before ground contact and extended into the early stretching phase of the triceps brachii. About 25 msec after contact was made between the ball of the thumb and the platform (*B*), there was a steep increase in activity lasting 80 msec. This enhanced activity was associated with the stretching phase of the triceps brachii, which ended some 150 msec after ground contact (*D*). Another constant finding was the steep

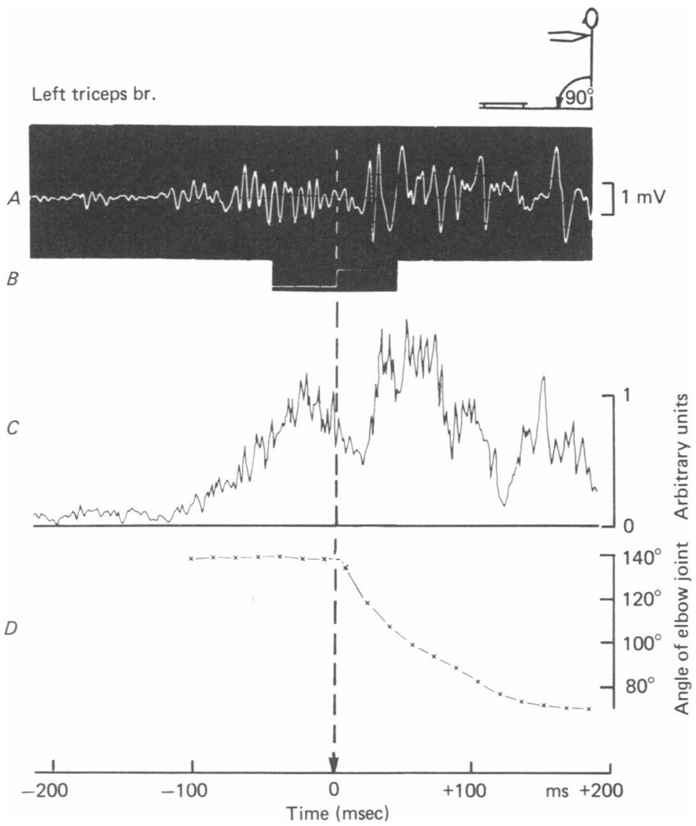

Fig. 1. Typical records obtained during a series of thirty falls forward (90°) on the arms as indicated by scheme on top right. All records from the left, non-dominant arm. *A*, *B*, *D*, single traces, *C*, average ($n = 30$). *A*, raw e.m.g. of the left triceps brachii (smoothed by filtering). *B*, step indicating moment of contact between ball of thumb and platform. *C*, averaged e.m.g. response. *D*, angle of elbow joint, determined cinematographically. In this and the following Figure, unless otherwise stated, records centred on moment of impact, as indicated by arrow and interrupted line. Improved landing platform used (see Methods). Athletic student.

increase in vertical platform force after touchdown (Fig. 2), followed by a trough and a slow recovery, which was completed when the angle of the elbow joint had attained a steady value. The platform force is, however, only a rough measure of the contractile force of the triceps brachii, as the inertia of the arm, force transformation at the elbow joint and the compliance and the natural frequency of the platform (Methods) must be expected to distort the force response to some degree.

Subjects falling forward on the arms without having received special instructions touched the ground first with the fingertips before contact was made with the ball of the thumb. This is the reason for the two-stage increase in vertical platform force after ground contact (see below, Fig. 3). When the subject was asked to land on the ball of the thumb with strong dorsiflexion of both hands during the fall, the force rose quickly to the maximum without initial creep (Fig. 2). Surprisingly, the quick flexion of the elbow joint did not coincide with the moment of touchdown, but was consistently delayed by 5–10 msec and occurred together with the peak of the quick tension rise.

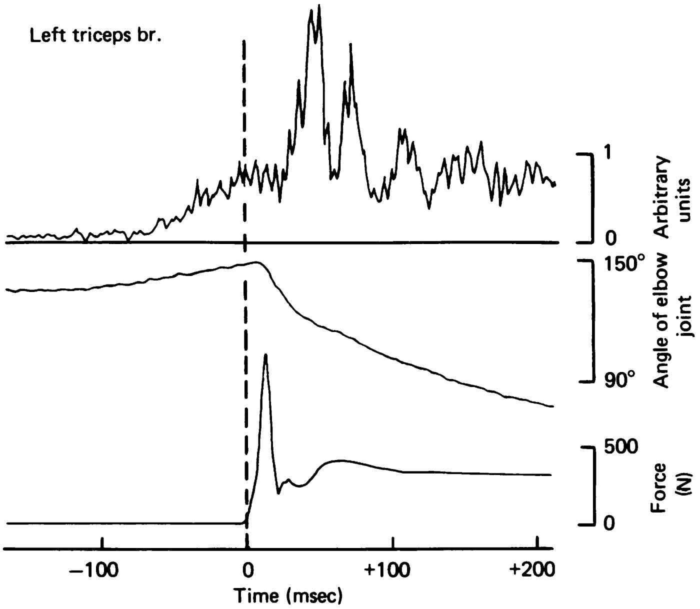

Fig. 2. Comparison between e.m.g. response (upper trace), goniometer signal (middle trace) and platform force (lower trace) for 70° falls ($n = 30$). First contact with platform (improved type) made by ball of the thumb, indicated by interrupted line. Athletic student.

In order to measure the latency of the early e.m.g. response, both the force record and the goniometer signal have been used for reference. The latency between impact (ball of the thumb) and first increase in e.m.g. activity ranged from 20 to 30 msec, and between onset of elbow flexion and increase in e.m.g. activity from 15 to 20 msec, respectively. The latter value agrees well with the latency obtained when the e.m.g. response was evoked by tendon jerks. For latency measurements, the falls were performed with strong dorsal flexion of both hands to ensure that first contact was made with the ball of the thumb.

The reproducibility of the early e.m.g. peak during a series of sixty falls to the ground is documented in Fig. 3. At the end of the series, the untrained subject was unable to decelerate the body completely without touching the platform with the body, which was due to fatigue of the shoulder and arm muscles. The occurrence of muscle fatigue is indicated by the smaller force development during the stretching of the triceps brachii after the initial force peak (*B*) in comparison to the start of the series (*A*), in spite of an increase in e.m.g. activity. The change in the e.m.g. profile with progressive muscle fatigue was mainly restricted to an increase of the pre-activity, which became larger, whereas the early e.m.g. response itself was not affected. No other consistent e.m.g. changes accompanying muscle fatigue have been observed.

When different falling angles (see Methods) were tested in one recording session with a subject knowing about the falling angles, it was found that the same general e.m.g. pattern prevailed (Fig. 4), but that some parameters were influenced by the depth of the fall. (1) The time elapsing from the start of the pre-activity up to the moment of impact became longer in deeper falls. (2) The strength of the pre-activity increased with increasing falling angles as did the activity level after the appearance of the early peak.

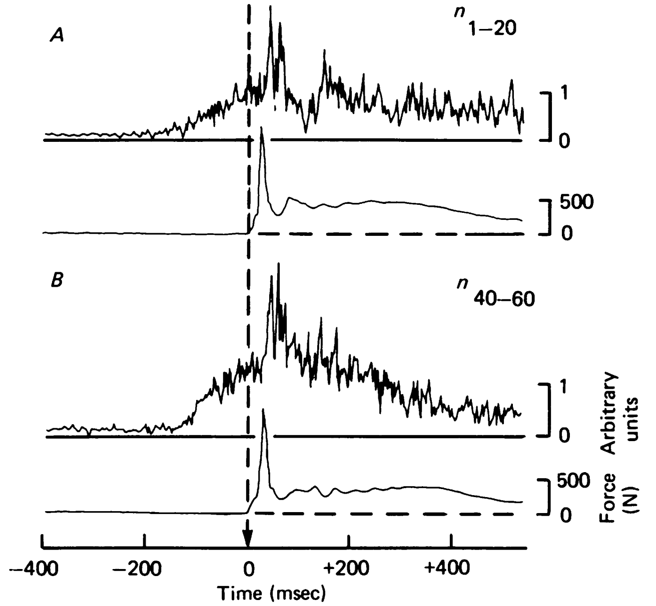

Fig. 3. Reproducibility of e.m.g. responses of left triceps brachii during a series of 60 falls (90°). *A*, averages of first twenty falls; upper record e.m.g., lower record vertical platform force exerted by left arm. *B*, averages of last twenty falls, records corresponding to *A*. Wooden platform placed on concrete ground. Right-handed, untrained subject.

The size of the early e.m.g. response, however, did not depend in a systematic way on the depth of the fall. Subjects exhibiting no distinct peak in the averaged e.m.g. with one depth generally did not do so with others. Marked differences in the e.m.g. pattern were often found between the right and left triceps brachii of the same subject. When the e.m.g. was recorded on several occasions from the same subject (four of whom were tested) with the electrodes at the same recording sites over the belly of the triceps on the same side, small but distinct differences in the patterns were also seen.

Later e.m.g. responses

Distinct later e.m.g. responses, as can be seen in Fig. 2, were observed in about 20 % of the e.m.g. profiles. The second peak appeared with a latency of 60–80 msec after impact and usually was followed by further peaks of decreasing height. In some cases regular peaks with a repetition rate of 20–30/sec persisted for 500 msec after impact. These 'oscillations' were found with both types of landing platform (see Methods). Damped platform oscillations are therefore not an essential requirement for the generation of these e.m.g. peaks. Distinct late responses were never seen without a detectable short-latency peak.

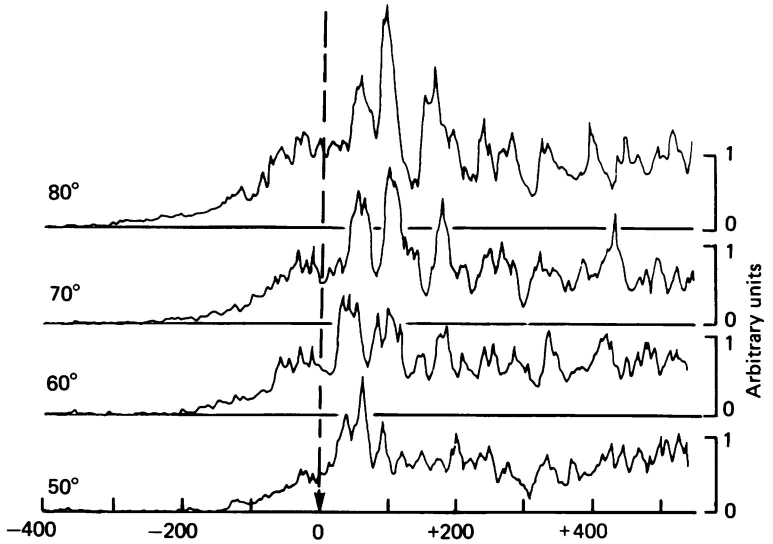

Fig. 4. Left triceps e.m.g. responses (averages of ten trials) during falls to different depths. Recording sequence from 50 to 80°. Arrow shows moment of impact, indicated by the simultaneously recorded and averaged strain gauge signal (not shown). Wooden landing platform. Left-handed, untrained subject.

E.m.g. pattern of the triceps during falls performed without visual control

It may be argued that the early increase in e.m.g. activity after impact is caused by a central programme utilizing the precise knowledge of the moment of ground contact, which would be most accurately anticipated by visual information. As shown earlier (Dietz & Noth, 1978), when the depth of the fall was not known and the subject was blindfolded, early e.m.g. responses could persist. These experiments have now been repeated with the improved platform (see Methods) allowing a more accurate evaluation of the latency of the response. Fig. 5 not only demonstrates the persistence of the short-latency responses in spite of the lack of any knowledge about the depth of the fall (see Methods), but also suggests that a large fraction of the e.m.g. activity after impact is reactive rather than pre-programmed.

This result shows that the early e.m.g. response is evoked by reflexes elicited at the moment of impact, the short latency of the response making it most likely that stretch receptors of the triceps brachii were involved. The sole responsibility of skin receptors of the hand could be excluded since the spinal stretch responses were little affected by ischaemic blockade of fast-conducting skin receptors of the hand by a pressure cuff around the wrist (Noth, Ledig, Schmidtbleicher & Dietz, 1978). The somewhat longer latency in the visually controlled falls in comparison to the blindfolded condition may be due to the higher pre-activity in the former (see also Fig. 4). In other cases, the difference was smaller or the pre-activity was even larger for deep falls with eyes closed.

The e.m.g. profile of forearm muscles during falls on the arms

Representative records of forearm flexors and extensors during falls are shown in Fig. 6. Similar records were obtained with two other subjects. Both flexors and extensors were pre-activated during the fall, but while the e.m.g. profile of the

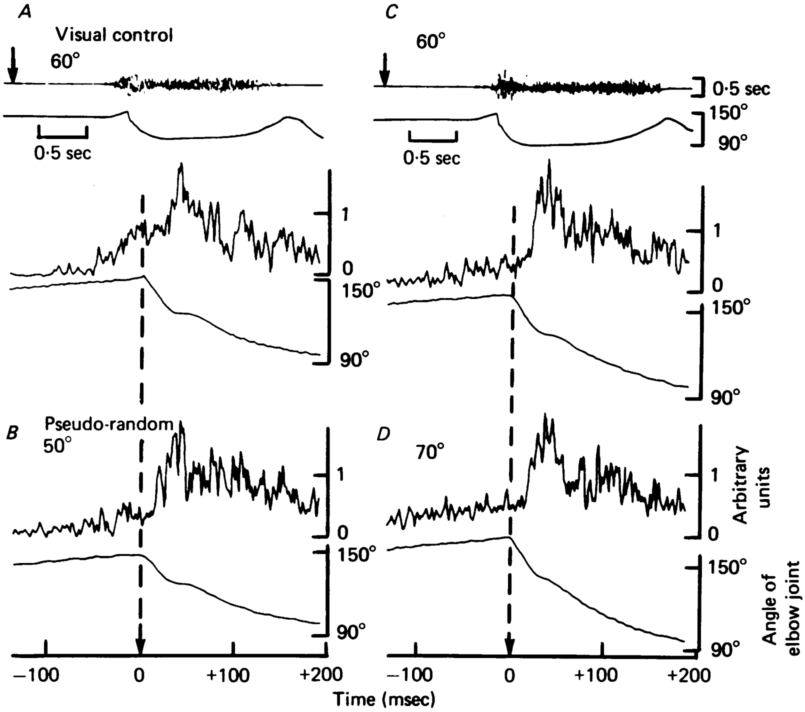

Fig. 5. Series of falls with pseudo-randomly varying depth of fall. *A*, control, depth of fall 60°. *B–D*, subject blindfolded, acoustic control excluded. Falls of 50, 60, 70° performed in a pseudo-random order. Two upper traces in *A* and *C* (original records) demonstrating smaller pre-activity in the randomized falls, arrow indicating start of the self-initiated fall. Note change in time scale. Goniometer signal was used for averaging the e.m.g. in *A–D*, averages centred on first downward deflexion of the goniometer signal. The time taken to fall between 60 and 70° was about 100 msec, measured separately with reference to the position of the hands. Improved platform. Right-handed, untrained subject.

forearm flexors mimicked that of the triceps brachii, the activity of the extensor muscles (which are, of course, functional flexors in this motor task) declined rapidly before the fingers touched the platform, and approached zero shortly after platform contact. The early onset of the decline argues against reflex inhibition as the only reason for this decay.

The early e.m.g. responses of the forearm flexors were, in general, shorter than the corresponding responses of the triceps brachii and usually consisted of only one or two peaks as in Fig. 6. In this context, it is important to note that the long finger flexors are stretched only during the short period up to the moment the ball of the

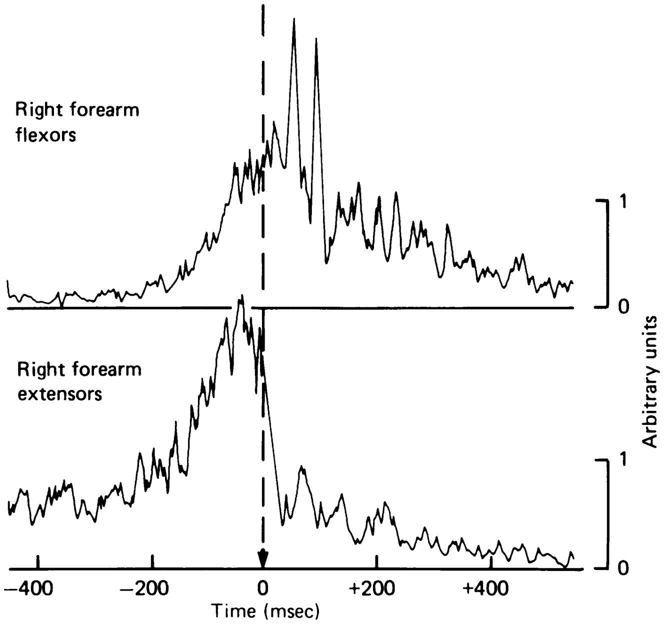

Fig. 6. Typical e.m.g. profiles of anatomical forearm flexors (upper trace) and extensors (lower trace) during 80° fall ($n = 10$). First platform contact was made with finger tips. Both e.m.g.s were recorded simultaneously with the same amplification. Note that, for this particular task, anatomical flexors are functional extensors and extensors are functional flexors. Wooden platform. Right-handed, untrained subject.

thumb makes contact with the platform. Therefore, the ongoing contraction of the forearm flexors may contribute to the stabilization of the wrist during the deceleration of the body.

DISCUSSION

The e.m.g. profiles obtained from the triceps brachii during forward falls onto the nearly extended arms exhibited the well-known pre-activity, starting shortly before impact. The functional implications of this activity have been discussed elsewhere (Engberg & Lundberg, 1969; Melvill Jones & Watt, 1971*a*). After impact, in the majority of observations early stretch responses appeared, which for several reasons may be taken to reflect true muscle activity. (1) Care was taken to detect and eliminate movement artifacts (see Methods). (2) High-pass filtering was used to suppress persisting slow base-line shifts. (3) The early e.m.g. responses appeared with a certain delay after impact, when abrupt displacements of the electrodes had probably subsided.

E.m.g. analysis

However, the peak of the early e.m.g. response might be unduly high due to synchonization of motor unit action potentials (for discussion see Matthews, 1972, p. 587). While this effect may be relevant for very short peaks, as found in response to tendon jerks, it is not likely to affect peaks lasting several times longer than the duration of the underlying action potentials, which is roughly 10 msec for surface e.m.g. recordings (Maranzana Figini, Bestetti & Valli, 1978). The compound muscle action potentials elicited by tendon jerks, which are of the order of 15–20 msec (Hoffmann, 1920), are markedly shorter than the early stretch responses described in the present work (Figs. 1, 2). Moreover, since the extracellularly recorded muscle action potentials are usually polyphasic, a small amount of dispersion of the individual components within the compound peaks might be expected to result in a similar degree of cancellation as occurs before impact. The averaged e.m.g. may therefore be taken as a rough measure of the activation of the motoneurone pool.

Origin of e.m.g. responses occurring after impact

Early e.m.g. responses were obtained in the absence of any information about the depth of the fall (Fig. 5). This excludes the possibility that a central generator is exclusively responsible. It rather appears that the responses represent the classical spinal stretch reflex evoked by the primary muscle spindle endings. This conclusion is further supported by the finding that the latency of the early response is roughly the same as that of the tendon jerk and that the responses persist after ischaemic blockade of skin receptors of the hand (Noth *et al.* 1978). Secondary muscle spindle afferents (Matthews, 1969) and other proprioceptors of the proximal arm and the shoulder girdle may, of course, participate later in the e.m.g. responses.

It is difficult to comment on the origin of the later responses. It seems important to note that whenever a later peak appeared it was preceded by a short-latency response. With regard to the latency (60–80 msec), the second response may well correspond to the functional stretch reflex. For the comparable biceps brachii, the second e.m.g. response begins around 50–60 msec after an unexpected increase in load (Hammond *et al.* 1956; Marsden *et al.* 1976*b*). The second peak may, on the other hand, be generated by motor units which discharge in synchronization. Synchronization could be caused either by a rebound after a fragmentary silent period following the early response (Alston, Angel, Fink & Hoffman, 1967) or by a tendency of motor units to discharge at similar rates after being recruited shortly after impact. The latter idea is supported by the occasional occurrence of long-lasting e.m.g. 'oscillations' during the lengthening period of the triceps brachii. The appearance of M 1, M 2 and M 3 responses in decerebrate and spinal cats (Ghez & Shinoda, 1978) substantiates the notion that later e.m.g. responses are not necessarily mediated by supraspinal pathways.

In the light of recent e.m.g. studies (Marsden *et al.* 1976*b*; Dufresne *et al.* 1978; Dietz *et al.* 1979; Crago, Houk & Hasan, 1976) and of the present results it must be asked, why in Hammond's (1960) experiments on stretch responses of the biceps brachii in man the early e.m.g. response was so small in comparison to the late response. It is unlikely that there is a basic difference between the response patterns of the antagonists which act on the elbow joint, because responses similar to those described here have also been found for the biceps brachii when it was stretched at high velocities by means of a torque motor (Dufresne *et al.* 1978). The way in which the motoneurone pool responds to change in the external load on the muscle it supplies may rather depend on the motor task and the kind of disturbance imposed on the muscle. In the classical experiments of Hammond *et al.* (1956), the speed of the imposed length change measured at the wrist was of the order of 40 cm/sec. This corresponds to about 80°/sec angular velocity of the elbow joint. The maximum angular velocity during the falls executed in the present experiments reached 800–1000°/sec (Figs. 1, 2, 5). Thus the difference in stretch velocity could explain why the spinal stretch reflex is so much more pronounced during a deep fall in contrast to moderate stretch velocities. The importance of the velocity of the imposed stretch for the magnitude of the spinal stretch reflex has recently been stressed by Gottlieb & Agarwal (1979) who found a linear relation between both parameters in the triceps surae in man. The same authors investigated the influence of the steady pre-activity on the magnitude of the early stretch response and found that the latter increased with higher voluntary force. Both factors, high stretch velocity as well as the existence of pre-activity at the moment of impact, might be responsible for the appearance of spinal stretch reflexes in the motor task of the present investigation.

Functional considerations

One argument against a functionally significant contribution of the spinal stretch reflex might be seen in the fact that subjects who exhibited no early e.m.g. peak were also able to perform the motor task without any difficulty. But the lack of a steep increase in the e.m.g. activity after touchdown does not necessarily exclude the presence of spinal stretch reflex activity during the deceleration phase of the fall. The apparent separation between the pre-activity and the early e.m.g. response will depend to some extent on the rate of rise of the afferent volley which evokes the response. Subjects able to land smoothly on their fingertips by strong pre-contraction of the finger flexors might use the stretch reflex without exhibiting the early increase in e.m.g. activity. This conclusion is supported by the finding that a higher incidence of early e.m.g. responses were observed with the concrete landing blocks than with the more compliant wooden platform, and that subjects landing on the ball of the thumb under the latter condition exhibited marked early stretch responses without any exception.

It is difficult to assess the extent to which the action of the spinal stretch reflex contributes to the force exerted by the triceps brachii during the deceleration of the body after ground contact. A muscle with pre-existing steady contraction is, of course, capable of developing additional tension in response to a forcible stretch. This tension consists of a transient overshoot at the beginning of the ongoing stretch (Nichols & Houk, 1976; Rack, 1970) and a more slowly increasing component due to the well known length–tension characteristics of the activated muscle (Rack & Westbury, 1969). The latter has been made responsible for the load compensation in various types of movements (Grillner, 1972; Gurfinkel, Lipshit & Popov, 1974). It is apparent from Figs. 1 and 2 that the initial force development, which to some extent may be produced by high initial muscle stiffness, is far from sufficient to decelerate the body completely. Instead, the elbow flexion begins after the initial force peak, and the entire deceleration phase lasts about 200–300 msec for deep falls. During this period, the spinal stretch reflex may serve to provide full activation of the triceps brachii.

Nichols & Houk (1976), working with decerebrate cats, demonstrated that the spinal stretch reflex markedly enhanced the late tension component during a ramp stretch of the soleus muscle. They further showed that the initial tension overshoot steeply increased with both higher levels of pre-existing contraction and higher stretch velocities. With the present motor paradigm, a maximal contraction of the triceps brachii at the moment of impact could thus lead to extremely high force peaks with the risk of bone fracture and tendon or muscle rupture. The spinal stretch reflex would ensure that, starting from a submaximal level, the muscle is fully activated as soon as the high initial muscle stiffness is reduced after impact.

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