European Journal of Neuroscience, Vol. 26, pp. 2204–2210, 2007 doi:10.1111/j.1460-9568.2007.05834.x

Mechanical and focal electrical stimuli applied to the skin of the index fingertip induce both inhibition and excitation in low-threshold *flexor carpi radialis* motor units

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Keywords: circuitry, cutaneous, human, sensory–motor integration, spinal reflexes

Abstract

It has been observed that mechanical stimulation of the skin of the index fingertip causes a weak short-latency inhibition followed by a strong long-lasting facilitation of the *flexor carpi radialis* (FCR) H-reflex. Based on threshold and latency, these cutaneous reflexes are thought to be routed to motoneurons by parallel pathways. As recent studies have shown predominant inhibitory potentials in slow motoneurons and predominant excitatory potentials in faster ones, the question arises as to whether or not the two cutaneous pathways converge onto the same motoneuron. The poststimulus time histogram technique was used to investigate the changes in firing frequency of low-threshold FCR motor units (MUs), induced by passive mechanical or focal electrical stimuli to the index skin. After gently tapping the finger pulp a small sharp inhibition appeared in 20 MUs. On average, inhibition started 10.2 ± 1.6 ms from the homonymous Ia monosynaptic effect, and its central delay was estimated to be 1.2 ± 1.6 ms. The subsequent facilitation, more consistent, had a mean latency of 13.5 ± 1.7 ms. Inhibition and excitation were statistically significant ($P < 0.05$). A similar biphasic effect was observed in seven other FCR-MUs, also after focal electrical stimulation of the same skin area. Comparison with the time course of the H-reflex, representing the whole population of MUs, showed striking similarities in time course and latency to the present MU effect. It is thus suggested that cutaneous spinal pathways may have a homogeneous distribution within the FCR motoneuron pool, and that the skewed distribution of cutaneous afferents onto motoneurons should be not taken as a rule.

Introduction

Many findings support the view that cutaneous afferents play an important role in shaping the motor output. In cats, convergence between cutaneous afferents and the corticospinal tract has been shown to occur on segmental and propriospinal pathways projecting to forelimb (Sasaki *et al*., 1996) and to hindlimb (Perrier *et al*., 2000) motoneurons. In man, tactile information from the hand has been shown to be essential in keeping the accuracy in pointing movements (Rao & Gordon, 2001) and in performing refined manipulation (Johansson & Westling, 1984, 1987; Lemon *et al*., 1995; Macefield *et al*., 1996; Jenmalm *et al*., 2000). Accordingly, cutaneous information is used to shape the finger movement itself but also to modulate a much broader action that may involve several joints (i.e. fingers, wrist, elbow and also shoulder). Moreover, it is also worth noting that input from one single cutaneous afferent is strong enough to drive the discharge of motoneurons supplying finger muscles (McNulty *et al*., 1999). The contribution of these reflex responses will therefore need to be considered when other inputs onto the motoneuron pool are being examined.

In man, H-reflex studies have shown that passive mechanical stimulation of tactile afferents from the index produces a weak short-latency inhibition, followed by a strong long-lasting facilitation, distributed within the *flexor carpi radialis* (FCR) motoneuron pool (Cavallari & Lalli, 1998). On the basis of threshold and latency, these cutaneous reflexes were supposed to be carried by two separate routes to motoneurons: a short-latency inhibitory pathway and a longer-latency excitatory pathway. From these last results a question arises as to whether the two pathways are distributed homogeneously in the pool, i.e. whether they both converge on the same motoneuron or whether the biphasic effect results from a mix of units, partly inhibited and partly excited. The same question also arise from the observation that animal studies have shown that stimulation of the sural and saphenous nerves evokes 'predominant' inhibitory postsynaptic potentials in slow triceps surae motoneurons, while 'a trend towards' excitatory predominance was found in the faster ones (Burke *et al*., 1970). A few human studies seem to parallel these results. Indeed, Garnett & Stephens (1980) have shown that electrical stimulation of the digital nerves of the index produces 'predominantly' inhibitory responses in slow twitch units and 'predominant' short-latency excitatory responses in fast twitch units of the first interosseus muscle. Similar results were reported for the tibialis anterior after stimulation of the sural nerve (Nielsen & Kagamihara, 1993).

To solve the puzzle and to better outline the organization of the two cutaneous reflex pathways influencing posture and gesture of the wrist, the poststimulus time histogram (PSTH) technique was used to assess the projections of tactile afferents from the index fingertip on single

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Received 18 April 2007, revised 16 August 2007, accepted 20 August 2007

motoneurons supplying FCR muscle. Surprisingly, our results show that a mix of excitatory and inhibitory effects from the index skin are distributed to single motoneurons, indicating that the skewed distribution of cutaneous afferents onto motoneurons should be not taken as a rule. Moreover, new evidence is produced about the tactile origin of the effects.

Materials and methods

Experiments were carried out on 36 FCR motor units (MUs) recorded from 16 healthy subjects (aged 22–49 years; seven females), all of whom had given written informed consent to the experimental procedures. The experiments were approved by the appropriate institutional ethics committees and were in keeping with the guidelines in the Declaration of Helsinki.

General procedure

Subjects were comfortably seated in an armchair. The right hand and forearm were in a prone position, lying on a horizontal support. The shoulder was in slight abduction (30°) and the elbow was semiflexed (110°). The index finger also lay on a small horizontal support with an open area (1 cm wide and 5 cm long) leaving the palmar side of the fingertip free for the mechanical stimulation (see below). The finger was securely fixed to the support at the distal interphalangeal joint by means of a Velcro band.

MU recording

Electromyographic (EMG) activity was recorded by surface electrodes (silver plates, 0.8 cm diameter, 2 cm apart) placed on the skin over the FCR muscle, which was identified by palpation and by voluntary wrist flexion and pronation. Subjects were asked to perform weak tonic contractions (1–2% of the maximal voluntary contraction) in order to isolate one single motor unit at constant and regular discharge frequency from those activated by the voluntary command. The recruited MUs were therefore all in the low-threshold range. EMG potentials were appropriately filtered and amplified before being A/D converted and used by the computer to trigger the cutaneous stimulation, about once every 0.5 s.

Histogram of the motoneuronal firing probability

The PSTH of a voluntarily activated FCR-MU was constructed for a period of 150 ms following the tactile conditioning stimulation (for details see Pierrot-Deseilligny & Burke, 2005). However, in these experiments a methodological improvement was introduced. In fact, before each conditioning stimulus was delivered, a number (two or three) of subsequent interspike intervals were automatically measured in order to predict the timing of the forthcoming MU potential. This calculation made it possible to deliver the tactile stimulus at a fixed percentage of the interspike period, i.e. always at the same level of the developing afterhyperpolarization. With this improvement an effect became apparent with a much lower number of MU counts, and statistical significance was reached faster.

Histograms of the firing probability (0.5-ms bin width) were automatically drawn for both the spontaneous and the conditioned discharge of each unit. Cutaneous stimulation was randomly alternated with spontaneous firing in the same sequence. Different experimental sessions were performed with mechanical and electrical stimuli. To highlight the effect of the conditioned stimulus, the spontaneous discharge was subtracted, for each bin, from the conditioned one.

Passive mechanical stimulation of the index skin

Mechanical taps (a 10-ms-duration rectangular pulse) to the resting right index fingertip were delivered by a small probe (diameter 200 μm) mounted on an electromagnetic vibrator (Brüel & Kjær 4809), driven by a power amplifier (Brüel & Kjær 2706). The intensity of the stimulus, expressed in multiples of the perceptual threshold (PT) for the cutaneous sensation, was set to 3 PT, at which the subject perceived a sensation of pressure without any discomfort or pain. Before starting acquisition, the probe was positioned as close as possible to the finger without any contact on the skin. The time necessary to overcome the mechanical delay of the hammer and the path of the tip in the air was constantly monitored by means of a simple electrical device. This consisted in an electric circuit, powered by a 9 V battery, connected by two copper plates to the index skin and to the probe. Thus, the contact between probe and skin produced a sharp change in voltage which was taken as the onset of the conditioning stimulus and is indicated as 0 ms in all figures.

Focal electrical stimulation of the skin

Focal electrical stimuli (a 0.8-ms-duration rectangular pulse) were delivered to the pulp of the right index fingertip by two rectangular copper strips (10 × 3 mm) placed a few millimetres apart from each other. The intensity of the stimulus was adjusted to 2 PT, i.e. an intensity at which the subject felt approximately the same tactile sensation produced by the mechanical stimulus at 3 PT, without any discomfort or pain.

Measurement of the afferent cutaneous volley

To evaluate the peripheral conduction time of the cutaneous volley in each subject, cutaneous evoked potentials were recorded from the median nerve at the elbow after focal electrical stimulation of the index at various intensities (from 0.8 to 3 PT). The potential was picked up by the same bipolar surface electrodes used to activate Ia FCR afferents (see below). The onset latency of the afferent volley was measured at the very first positive peak.

Mechanical extension of the index finger

For this conditioning situation, the support for the index (see above) was removed and the digit was positioned horizontally and fixed securely at the distal interphalangeal joint by a rigid clamp mounted on the electromagnetic vibrator (Brüel & Kjær 4809). A vertical displacement of the clamp (10-ms-duration single rectangular pulse) induced a brisk extension of the finger around the metacarpophalangeal joint. The amplitude of the extension was regulated by the power amplifier, and ranged between 0.5 and 3 mm.

Electrical stimulation of the median nerve

Monosynaptic excitation of FCR-MUs (see below) was elicited by surface electrical stimulation of the median nerve in the cubital fossa (bipolar silver electrodes, diameter 8 mm, placed 1 cm apart, cathode proximal). Rectangular pulses of 1 ms duration were set at 0.6–0.95× motor threshold. This early effect was measured in all MUs and its latency used to estimate the shortest synaptic effect on that MU.

Statistical analysis

In each trial, the difference in firing probability was computed by subtracting the spontaneous motor unit discharge from the conditioned response. This computation allowed identification of periods of reduction or increase in firing probability, which should correspond to an inhibitory or an excitatory effect on the motoneuron (see Gustafsson & McCrea, 1984). To identify the onset of an effect, the cumulative sum technique (see Ellaway, 1978), coupled to the Monte Carlo method (see Ushiba *et al.*, 2002), was used. In fact, with this procedure the operator can set the limit of the windows in which a statistical analysis will be performed. Consecutive bins of the same sign (inhibitory or excitatory) were then grouped, and the χ^2 test used to assess to what extent the distribution of the firing probability after conditioning differed from that obtained in the control situation (for further details see Pierrot-Deseilligny & Burke, 2005).

The size of the effect (expressed as a percentage of the total number of spontaneous triggers) was obtained by summing the value of consecutive bins with decreased or increased firing probability. Grouped data are expressed as mean ± SD.

Results

Mechanical conditioning stimuli to the index fingertip were used to modulate the discharge of 20 FCR-MUs. Seven additional units were conditioned by focal electrical stimuli to the index skin. The remaining nine units were conditioned by a finger extension (see below).

Both mechanical (passive finger tap) and focal electrical stimulation of the skin produced a short-latency inhibition followed by a long-lasting excitation in every recorded unit. Figure 1 illustrates the changes in the firing probability of individual FCR-MUs, recorded in one subject, after each kind of stimulus. To highlight the effect of the cutaneous conditioned stimulus, the MU spontaneous discharge was subtracted, for each bin, from the conditioned one.

Mechanical stimulation of the skin of the index fingertip

Mechanical taps to the skin at an intensity of 3 PT induced a clear biphasic effect in the FCR-MU discharge (Fig. 1A, black columns). Indeed, a tiny inhibition (2% of the total number of triggers) began ~38.0 ms after the conditioning stimulus delivery and lasted for 2.5 ms. Inhibition was followed by a large facilitation (19% of the total number of triggers), starting 40.5 ms after the stimulus and lasting 9.5 ms. Both effects were statistically significant ($P < 0.05$). Note that the effect recorded in single motoneurons strictly matches that observed with the H-reflex technique (Cavallari & Lalli, 1998). This is true both for the time-course and for the size of the inhibitory phase as compared to the excitatory one. If matched to the latency of the earliest Ia homonymous effect on the same unit (26.5 ms, Fig. 1B), cutaneous inhibition needed an additional 11.5 ms to develop, a delay which includes the time difference due to the peripheral position of two conditioning stimuli. Thus, in each subject, the conduction time of the afferent cutaneous volley from index finger to elbow was measured (see Materials and methods) and its value subtracted to estimate the central delay of the very first effect. In the case reported above, the central delay was calculated as 2.0 ms, as the peripheral time difference from finger to elbow was 9.5 ms. Such a short central delay is thus compatible with an oligosynaptic transmission in the spinal cord. The central latency of the facilitatory effect was more difficult to estimate because of the probable overlap between the inhibitory and facilitatory phases. For this reason, the central latency of the facilitatory effect was not computed and only the delay from the Ia monosynaptic facilitation (in this case 13.5 ms) is be presented.

A qualitatively similar biphasic effect was observed in 20 FCR-MUs collected from eight subjects. The mean central latency of inhibition (with reference to Ia monosynaptic excitation and after purging both the contact time and the peripheral delay) was 1.2 ± 1.6 ms. The subsequent facilitatory phase becoming apparent 13.5 ± 1.7 ms from the monosynaptic effect. Mean duration of inhibition was 2.8 ± 1.3 ms, while excitation lasted 6.3 ± 2.6 ms. In all subjects inhibition was always weaker than excitation: on average the inhibitory effect reached 3.2 ± 2.3% of the total number of spontaneous triggers, while facilitation was ~3–4× larger (11.4 ± 7.2% of the total number). Note that, because of the smaller number of counts associated with the initial inhibition, the subsequent large facilitation cannot be seen simply as a rebound phenomenon.

Focal electrical stimulation of the skin of the index fingertip

Figure 1C illustrates the effect evoked by a focal electrical stimulation of the skin of the index fingertip at 2 PT. Note that, although smaller in amplitude, the conditioning stimulus produced on FCR-MUs a sequence of short-latency inhibition and later excitation. In this case inhibition began at 33 ms and was followed by an excitation, occurring 2 ms later and lasting 3 ms. Both effects were statistically significant ($P < 0.05$). After matching with the latency of the Ia monosynaptic excitation (21.5 ms; Fig. 1D), the latencies of the inhibition and excitation were 11.5 and 13.5 ms, respectively. Again, the central latency of the very first inhibitory effect (1.7 ms) was compatible with an oligosynaptic linkage.

Such a biphasic effect was observed in seven FCR-MUs collected from five subjects. The mean latency from the Ia monosynaptic excitation was 10.1 ± 1.2 ms and, for the inhibition, 12.0 ± 1.1 ms. The duration of the inhibitory phase was 2.8 ± 1.6 ms while facilitation lasted 4.1 ± 1.8 ms. Also in this case inhibition was weaker in amplitude than excitation (2.6 ± 0.9 and 4.8 ± 2.1% of the total number of spontaneous triggers, respectively).

Brisk extension of the index finger

In our methodological conditions it is hard to exclude the possibility that, in addition to the cutaneous activation, mechanical stimulation of the index finger may have caused a slight stretch, or vibration, of other forearm and hand muscles which could have resulted in a heteronymous facilitation of the FCR-MU. To exclude this undesired effect, we intentionally stretched the finger flexor with a strong mechanical stimulus and we recorded the ensuing changes in the FCR-MU firing frequency. Figure 2 illustrates the result of this experiment, in a single subject, when using two different stretch intensities. A brisk extension of 0.6 mm of the metacarpophalangeal joint (three times larger than the stimulus used with the cutaneous stimulation) produced a strong facilitation of the FCR-MU firing frequency (21% of the total number of triggers; Fig. 2A), with a latency of 26.5 ms. The amplitude of this facilitation was more than doubled when the finger extension reached 1.8 mm (55% of the total number of triggers; Fig. 2B). Note also that in this last case the latency of the effect shortened from 26.5 to 25.5 ms. If compared to the monosynaptic action evoked by electrical median nerve stimulation at the elbow (16.5 ms; Fig. 2C), the latency of this heteronymous facilitation measured 9 ms.

Such an excitatory effect was observed in nine FCR-MUs, recorded from nine subjects, and was always highly statistically significant ($P < 0.001$). Its mean latency was 10.3 ± 1.6 and its duration 3.8 ± 1.5 ms. This finding is compatible with monosynaptic excitation

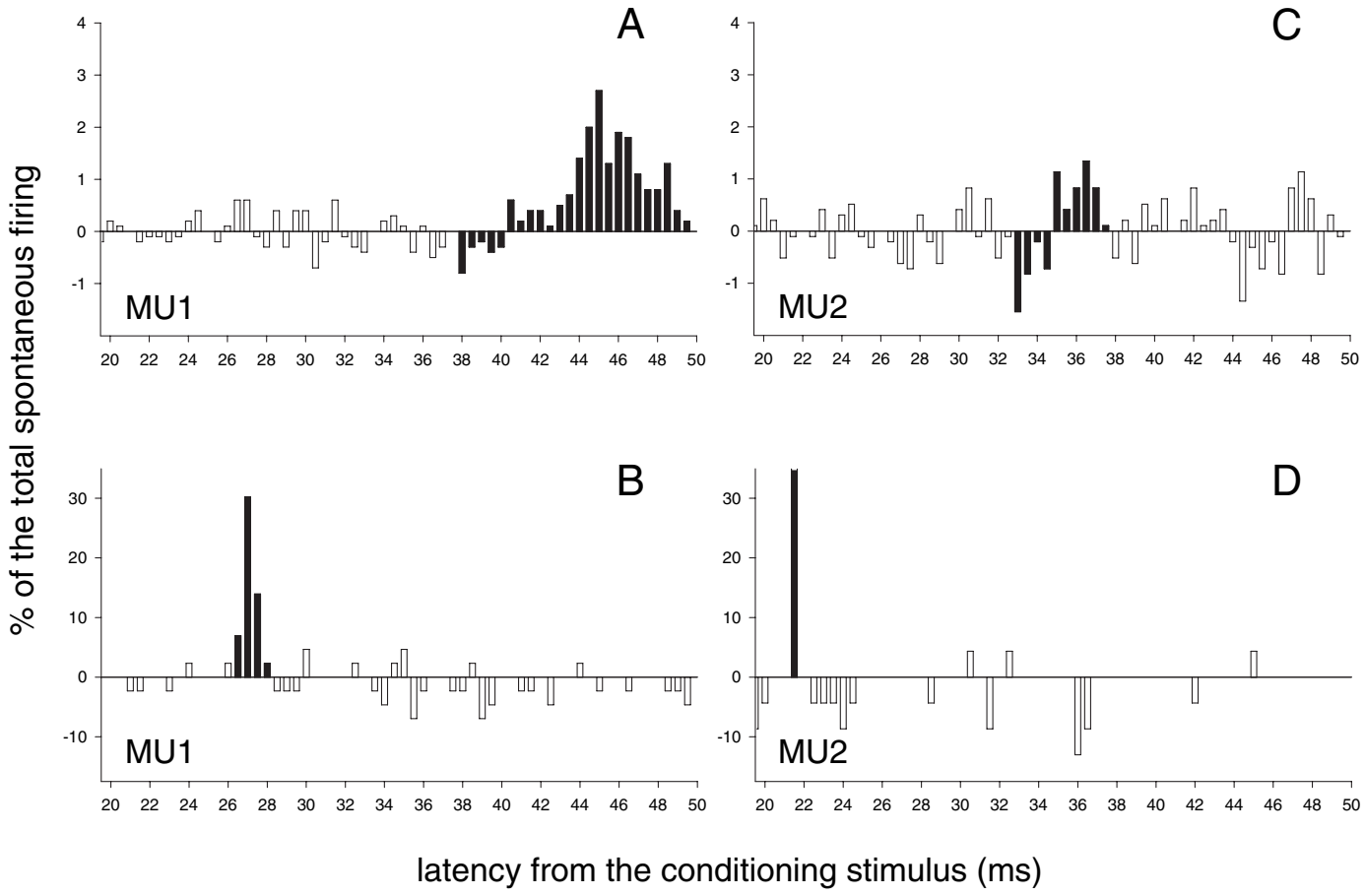

FIG. 1. Mechanical and electrical stimuli to index skin produced both inhibition and excitation in the same FCR-MU. (A) The biphasic effect obtained after cutaneous mechanical stimulation is matched with (B) the monosynaptic Ia excitation evoked in the same unit by median nerve stimulation at the elbow. Black columns denote statistically significant bins ($P < 0.03$). Note that the cutaneous effect has a central delay of 2 ms, after subtraction of 9.5 ms, i.e. the finger-to-elbow peripheral conduction time. (C and D) Effects of focal electrical stimulation and the companion monosynaptic Ia excitation are shown for a different unit. Note the similarity in latency and shape between mechanical and electrical effects. All panels display the algebraic difference between the histogram of the conditioned firing and that of the spontaneous discharge (1000 triggers in each condition).

evoked by Ia afferents. In Fig. 2D is also depicted the modulation of the excitatory effect (as a percentage of its maximum) as a function of the stretch amplitude. Note that the threshold for the effect was ~ 0.6 mm stretch and that the slope of the curve was very high, up to 1.2 mm, and reached a plateau for stronger stimuli. Thus, all these data suggest that mechanical and electrical stimulation of the index pulp mainly excite cutaneous afferents.

Comparison of data obtained with the PSTH technique and H-reflex

Figure 3 has been prepared by pooling the effects obtained separately in the 20 FCR-MUs, conditioned by the mechanical cutaneous stimulation, described above. The sum has been done after synchronizing the units on the point where inhibition switched to facilitation (0 ms; Fig. 3). Finally, this 'multiunit' PSTH (grey bars in Fig. 3) has been superimposed (always centred on the switching point) on the time course obtained with the H-reflex technique by Cavallari & Lalli (1998; black dots). We are aware that this procedure is not 'orthodox' and it disrupts important information about latency and duration of the effects; however, it allowed us to reconstruct the behaviour of a virtual population characterized by only small FCR motoneurons. It is apparent that the effect profiled by the 'multiunit PSTH' matches in a striking manner that obtained with the H-reflex, not only with respect to their course but also with respect to the inhibition : facilitation ratio, which is on average $\sim 41\%$ for the H reflex curve and 42% for the PSTH. The impressive matching between the two results (see Fig. 3) allows us to infer that cutaneous stimulation also produces the same inhibitory–facilitatory effect in larger FCR-MUs, not studied in the experiments reported here but certainly recruited within any H-reflex response.

Discussion

The aim of this study was to answer the question whether the cutaneous inhibitory and the excitatory pathways from the index skin to FCR both converge on the same motoneuron, or the biphasic effect derives from a mixture of 'predominantly' inhibited small units and 'predominantly' excited large units. In contrast with previous results, here we show that the mechanical stimulation of cutaneous mechanoreceptors of the index finger induces a biphasic modulation of the discharge in every single low-threshold FCR-MU analysed; an effect similar, in its course and its size, to that observed in the motoneuronal population by means of the H-reflex testing (Cavallari & Lalli, 1998). The skewed distribution of cutaneous afferents onto motoneurons,

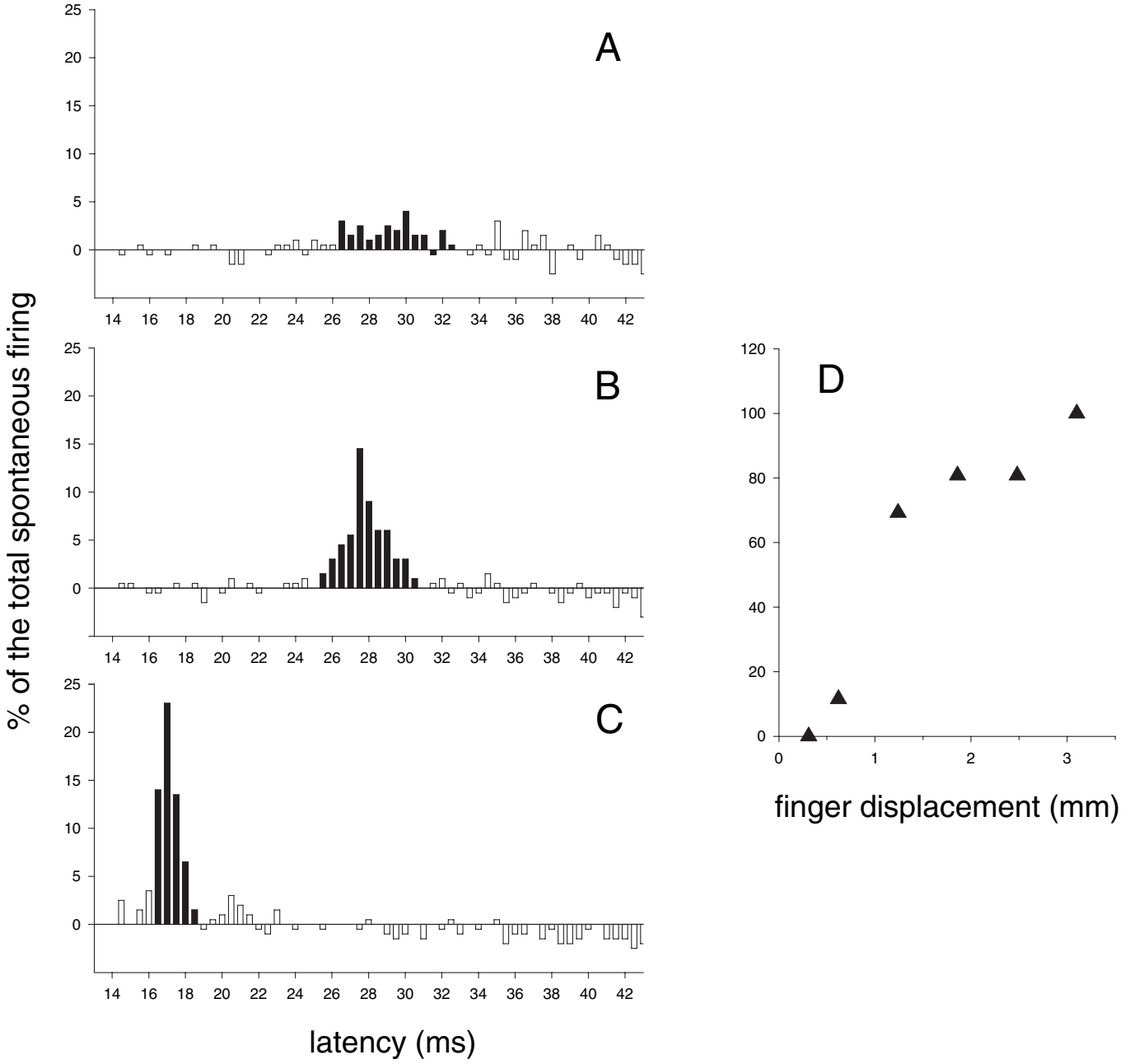

FIG. 2. Brisk extension of the proximal phalanx of the index produced heteronymous facilitation of FCR-MU. The excitation obtained after (A) a tiny (0.6 mm) or (B) a large (1.8 mm) stretch, applied to finger II, is matched with (C) the monosynaptic Ia excitation, evoked in the same unit by median nerve stimulation at the elbow. The stretch effect developed 9 ms after Ia monosynaptic excitation, i.e. it was very probably oligosynaptic in origin. Black columns denote statistically significant bins ($P < 0.03$). All panels display the algebraic difference between the histogram of the conditioned firing and that of the spontaneous discharge (1000 triggers in each condition). (D) Stretch reflex intensity curve is plotted black triangles.

described both in cat and man (Burke *et al*., 1970; Garnett & Stephens, 1980; Nielsen & Kagamihara, 1993), should thus not be taken as a rule. The study also provides new evidence about the tactile origin of the effects. The functional role of these circuits will be briefly discussed.

Homogeneous distribution of the effect into the motoneuron pool

Cutaneous inputs have been shown to have a skewed distribution on motoneurons innervating early- and late-recruited MUs (Garnett & Stephens, 1980; Nielsen & Kagamihara, 1993). In particular, Garnett & Stephens (1980) have shown that an electrical stimulation of low-threshold cutaneous afferents from index digital nerves produced a reflex response onto first dorsal interosseus MUs consisting of three phases: early excitation (E1), followed by an inhibition (I1), followed by a second late excitation (E2). They also showed that the magnitude of the early excitatory response, on the one hand, and the early inhibitory and late excitatory responses, on the other, were related to the level of the voluntary contraction produced by the subject, thus indicating a skewed distribution of the effects on slow and fast units. Naturally, these results made us

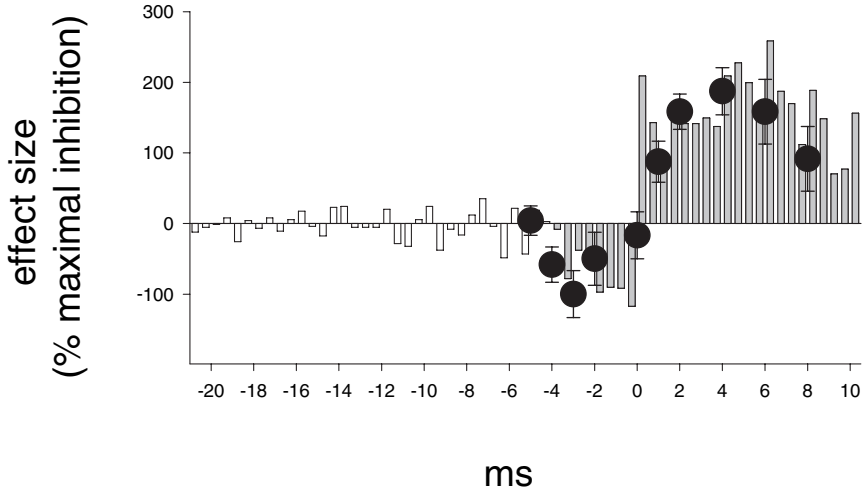

FIG. 3. Effect of mechanical stimulation of the index finger skin as revealed by our population of MUs and by an H-reflex. Grey bars depict the average biphasic time course, measured on 20 FCR-MUs, after synchronizing them when inhibition switched to facilitation. Superimposed black dots show the same effect when tested by an H-reflex elicited in the FCR muscle. Because of its low threshold, this 'fictive' MU population should be recruitable in H-reflexes of any amplitude.

wonder whether the cutaneous effects described here have the same origin and the same functional significance as those described by Garnett & Stephens (1980) or whether we are facing another case of skewed distribution of the input to motoneurons recruited at different threshold levels.

First of all, it is apparent that the FCR and first dorsal interosseus effects display different time courses: triphasic for the Garnett & Stephens (1980) one and only biphasic in our case. Second, based on their latency, it is very difficult to argue that our inhibition and the following facilitation are equivalent to the Garnett & Stephens (1980) 'phases I1 and E2'. This matching is complicated by the fact that these authors did not measured latencies from the Ia monosynaptic effect, as we did, but from the latency of M and F waves. However, if one is compelled to match the latency of the effect produced by our focal stimulation of the skin to that produced by their stimulation of the digital nerves (another difference which may slow down our latencies), the first one has a mean delay of 10 ms from the FCR monosynaptic Ia excitation while the second is on average 6 ms longer than the latency calculated from F and M waves (see page 353 of Garnett & Stephens, 1980). Indeed, this last delay should be lengthened by $\sim$4 ms to compensate for the differences in position of the recording electrodes, which we placed over the FCR muscle and they placed over the first interosseus dorsalis ($\sim$ 25 cm distance and $\sim$65 m/s conduction velocity; see Marque *et al*., 2001). After this correction, our inhibition would be synchronous with the earliest Garnett & Stephens (1980) excitation. Third, it is also evident that duration of E1 is considerably longer than our inhibitory effect (11 vs. 2 ms, respectively), and covers approximately the whole time course we described. The discrepancies listed above imply a different functional role of the pathway we describe, which has another exclusive characteristic, i.e. it regulates transjoint cutaneous reflex actions. One last argument derives from the comparison between data obtained with the PSTH technique and those obtained with the H-reflex (see Results).

In conclusion, we are aware that it will also be of interest to investigate the effectiveness of early inhibition and late excitation in high-threshold MUs. However, there are at least two reasons not to have considered this aspect in the present paper. The first is that this is a preliminary observation aiming to resolve whether the two cutaneous pathways are distributed homogeneously in the same units recruited by the H-reflex. The second reason is methodological: in fact, with the PSTH technique, only units recruited at very low levels of force may be selectively analysed.

New evidence about the cutaneous origin of the effects

Despite the convincing result obtained with skin anaesthesia (Cavallari & Lalli, 1998), one may worry about an eventual activation of muscle spindles due to the mechanical skin indentation. In fact, the light tap on the fingertip may have spread to muscles via bone transmission (Matthews, 1972) and contaminated the excitatory cutaneous effect. However, the matching effect obtained with the focal electrical stimulation is a strong argument against this hypothesis as in that case no vibration is produced. Although the electrical stimulation of the digital nerves failed to induce changes on the FCR H-reflex (Cavallari & Lalli, 1998), here it is demonstrated that focal electrical stimulation of the index skin produces a sequence of inhibition–excitation similar to those evoked by mechanical stimulation, with a very similar central latency of the first inhibitory effect. This last result supports the hypothesis formulated by Cavallari & Lalli (1998) that direct activation of fibres arising from mechanoreceptors may be more efficient than stimulation of the whole digital nerve. Although both focal electrical and mechanical stimuli induce a biphasic modulation of the FCR motoneuron excitability, differences in the size and duration of the excitatory effect were observed: excitation due to mechanical stimulation was more powerful than that obtained after the electrical one. Indeed, it may be proposed that low-intensity mechanical stimulation may activate the more superficially located receptors while electrical stimulation would activate synchronously and aspecifically the entire pool of afferent fibres. This possibility is also supported by the work of McNulty *et al*. (1999), in which is it is demonstrated that cutaneous afferents arising from different mechanoreceptors can induce different modulation in EMG, and by the paper of Tamburin *et al*. (2005), in which it is reported that stimulation of large cutaneous fields is less effective than that of

small cutaneous fields in producing inhibition of FCR corticospinal excitability. In conclusion, we have several lines of evidence which exclude the possibility that the late facilitation is produced by stretching of flexor muscles. First, the displacement of the index finger, which may have occurred during mechanical stimulation of the skin, is abundantly below the threshold for the excitatory heteronymous effect. It is also necessary to take into account that the finger was tightly fixed at the distal interphalangeal joint by the Velcro band. Second, the latency of the facilitatory heteronymous effect was 3 ms shorter than that of the facilitation produced by mechanical stimulation of the skin. Third, if one takes into account that the heteronymous effect should include the delay due to the hammer, and the finger inertia, the difference in latency would be larger than that calculated above.

Opposite effects evoked by cutaneous afferents: a possible functional role

Classically, tactile afferents have been considered to subserve various tasks in the regulation of movement control, the most intuitive being the regulation of force level during grasping and the interruption of motion when a target is reached. The idea that cutaneous afferents may play a crucial role in curtailing movement was originally proposed by Lundberg *et al*., (1977), who observed that stimulation of cutaneous afferents facilitates the Ib inhibitory pathway in the cat hindlimb. However, in several motor tasks the same touch signal could also be used to excite, more than inhibit, motoneurons, thus prolonging the ongoing contraction. For example, during precision and power grip actions, activation of antagonistic wrist muscles is necessary to stabilize the wrist posture (see Pierrot-Deseilligny & Burke, 2005).

The fact that cutaneous afferents can alternatively inhibit or excite motoneurons should not be surprising as experiments on reflex activity during movements have shown that the action from specific sensory inputs are re-routed and mediated via different neuronal networks (Hultborn, 2001). Accordingly to the task-dependent modulation of the sensory feedback, our biphasic effect meets a very simple functional explanation. When hitting an obstacle during an exploratory movement, the cutaneous feedback may be routed to the spinal pathway that mainly produces inhibition of FCR motoneurons. However, one can also easily imagine that facilitation should prevail when the subject simply wants to grasp the target object. The behavioural context in which the cutaneous reflexes are elicited, and thus the central modulation of the spinal excitability, would favour one of these of two effects by switching the information to the appropriate set of interneurons, as happens for example during locomotion (see Orlovsky *et al*., 1999).

Acknowledgements

This study was supported by grants from the Ministero dell'Università e della Ricerca and from the Università degli Studi di Milano.

Abbreviations

EMG, electromyogram; FCR, *flexor carpi radialis*; MU, motor unit; PSTH, poststimulus time histogram; PT, perception threshold.

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