Neuroscience Letters 440 (2008) 193–196

Contents lists available at ScienceDirect

Neuroscience Letters

journal homepage: www.elsevier.com/locate/neulet

High frequency tendon reflexes in the human soleus muscle

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ARTICLE INFO

Article history:
Received 10 March 2008
Received in revised form 17 April 2008
Accepted 20 May 2008

Keywords:
Tendon tap
Vibration
Reflex
Vibration burst
Percussion

ABSTRACT

Tendon reflexes have been often used in studies of the human nervous system in health and disease. They have been investigated either in response to single tendon taps or to long duration vibrations. Tendon reflexes are described here in response to a high frequency vibration burst (3 cycles of a 100 Hz sine wave) applied to the Achilles tendon of standing subjects, either in quiet stance or during a forward leaning posture. The electromyogram from the soleus muscle usually showed three components separated by 10 ms which were interpreted as being three reflexes, each reflex induced by each of the three cycles in a burst. This result indicates that soleus tendon reflexes can respond in fast succession in a phasic manner when a brief high frequency vibration is applied to the Achilles tendon. This occurs in spite of possible depression of the Ia to motoneuron synapses and the long after hyperpolarization of the motoneurons. An interpretation of the results is that motoneurons from different subsets of the motoneuron pool respond to different cycles of the sinusoidal vibratory burst.

Tendon reflexes have been frequently used in the investigation of the human nervous system [15,25,30,32,33]. In a recent report [3], experiments employing tendon tap together with prolonged vibration and single motor unit analysis suggested that the gain of the gamma loop is increased during fatigue. Tendon vibration (e.g., of the soleus muscle) has been an important tool in the study of the mechanisms behind postural control in humans [1,4,8]. High frequency (e.g., 100 Hz or higher) vibratory stimulation of a tendon may evoke the tonic vibration reflex (TVR) that has been employed as a tool for understanding peripheral and central mechanisms in the human nervous system, and also to evaluate nervous system disease [7,10,23,24,31]. A recent report [8] showed a statistically significant level of TVR in restrained standing subjects that had their Achilles tendon vibrated at 90 Hz. The subjects reported postural illusions in response to the tendon vibration. The soleus EMG interference pattern (see their Fig. 2) during the 90 Hz vibration indicates clearly that the motoneuron pool is being activated strongly by the spindle afferents. As the EMG mean integrated level during the TVR is higher than during control, it is clear that extra motor units must be recruited by the vibration during the whole duration of the applied vibratory stimulus. However, as the TVR needs a relatively long time to build up after the vibration is switched on [20] the question that may be posed is how does the motoneuron pool respond to a very short vibration applied to the Achilles tendon. The phasic stimulus adopted in this paper is composed of only three cycles of a 100 Hz sinusoidal vibration – a *vibratory burst* – of duration 30 ms. Is the motoneuron pool able to respond quickly to the vibratory burst? Will it generate only a single reflex in response to the burst or a reflex for each cycle of the burst? If the latter is shown by the experiments, i.e., the motoneuron pool responds in fast succession to each cycle within the burst, this evidences that the link between spindle afferents to muscle fibers is fast and reliable in transmitting high frequency sensory information. Hence, in response to such a vibratory burst, one may have the following cases: no reflex, one reflex, two reflexes (for cycle-pairs 1–2, 1–3 or 2–3), three reflexes, or, more than three reflexes. The first case may certainly occur when the vibration amplitude is low and is of no particular interest. The last case would imply some slow mechanism that allows accumulation in a variable, like in the genesis of plateau potentials [17]. The experiments to be described here showed cases with one, two or three reflexes per burst.

Thirteen subjects (age 31.4 ± 8.7 years) were tested while standing quietly on a flat and hard surface. Some subjects were also tested while leaning forward and putting more weight on the right leg. The experiments had approval by the local ethics committee and were conducted in accordance with the Declaration of Helsinki. Each subject signed an informed consent document. The Achilles tendon of the right leg (all subjects were right-footed) was stimulated mechanically by means of a Labworks vibration system, model LW-126-13, consisting of a power amplifier and a shaker (cylindrical body, with diameter 10.5 cm and length 13.5 cm). The shaker was fixed rigidly to the lab's elevated floor and the subject was standing barefoot on a platform fixed to the lab's floor (this avoided

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doi:10.1016/j.neulet.2008.05.075

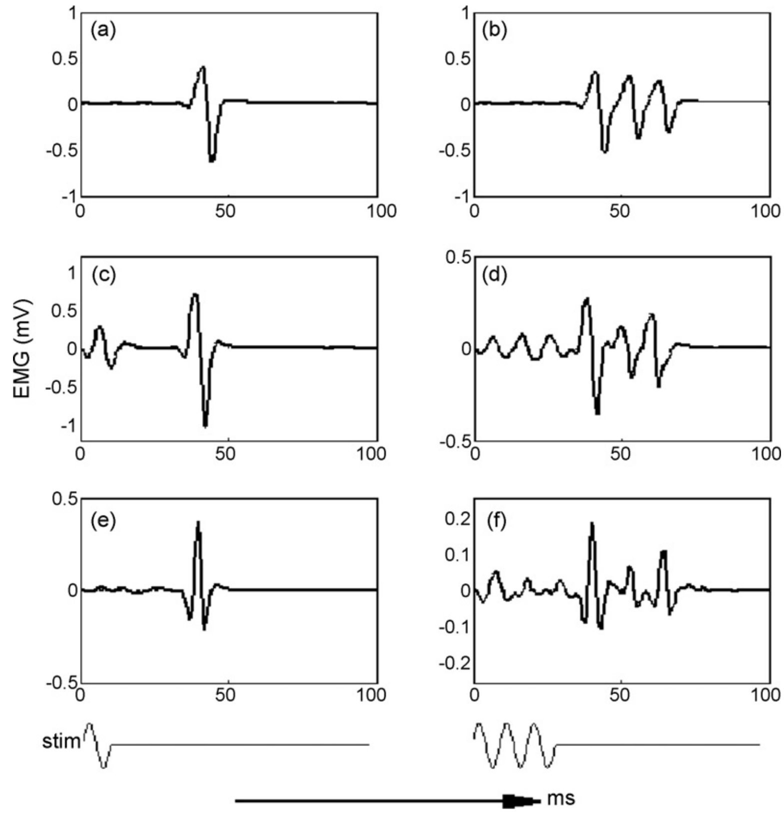

Fig. 1. Average of 50 responses recorded from three subjects (first: a, b; second: c, d; third: e, f) subjected to a one-cycle vibration (a, c and e) or three cycles of 100 Hz vibration applied to the Achilles tendon (b, d and f). In some cases there is a clearly visible stimulus artifact at short latencies. For the single cycle vibration there was a single component in the EMG response, while for the vibration burst there were three components.

vibration to spread from the shaker to the subject's foot soles). A customized disk-shaped plastic tip (1 cm diameter) was attached to the shaker's vibrating end and touched the tendon. The tip of the shaker was pressed against the Achilles tendon so that the steady pressure could keep the shaker's tip at a fixed position on the tendon during a sequence of vibration bursts. The place of mechanical contact along the tendon was searched for each subject so to ensure an efficient mechanical stimulation that induced a reflex contraction. A customized signal generator was connected to the input of the power amplifier to generate a 3-cycle 100 Hz sinusoidal burst with duration of 30 ms. In some subjects the shaker's mechanical output exhibited an extra cycle, albeit of smaller amplitude, due to the dynamic response of the shaker–tendon system. A trigger pulse occurring at every 2 s synchronized the occurrence of each sinusoidal burst and the start of the EMG signal acquisition from the soleus muscle by a LabView program. The EMG of the soleus muscle was recorded with two cup electrodes (0.8 cm diameter) fixed with an electrolytic gel to the skin 4 cm and 6 cm below the junction of the two heads of the gastrocnemii. The EMG was amplified and filtered (5–1000 Hz) by a Nihon-Kohden MEB 4200 system with its analog output being A/D converted by a National Instruments board at 2500 samples/s. The mechanical stimulus intensity was set for each subject so that a clear reflex muscle twitch could be perceived visually. The peak-to-peak acceleration of the burst of vibration used in this study was 200 g in the average (200 times the acceleration of gravity). This corresponded to a peak-to-peak displacement of the tip of the shaker around 5 mm. Each EMG acquisition window of 2 s duration comprised 5000 samples in response to every 3-cycle sinusoidal burst percussion of the tendon. For each subject 50 responses were acquired and analyzed in the Matlab environment, totalizing 100 s per experiment. In each EMG acquisition window there was a stimulus artifact due to the electromagnetic coupling from the shaker to the recording electrodes. Individual responses to a single vibratory burst were analyzed as well as the time-aligned average over the 50 responses. For control purposes, a single cycle of a 100 Hz sinusoid (10 ms duration) was applied in some subjects at every 2 s for a period of 100 s.

When a single cycle of a sinusoidal vibration of sufficient amplitude was used, a clear muscle twitch was visible on the tested leg and the corresponding EMG showed a single component, as shown in Fig. 1a, c and d (averages of 50 repetitions) for three subjects. The basic muscle compound action potentials in Fig. 1a, c and d in response to a single cycle vibration exhibited the classic bi or triphasic morphology. Fig. 1b, d and f shows the average EMG responses for a three-cycle vibration burst of the same subjects whose responses to a single cycle vibration are seen at the left column of Fig. 1. Three components are clearly seen in those responses, with an average inter-component interval around 10 ms. The first component of the three seen in Fig. 1b, d and f was similar in shape to the corresponding reflex response to a single cycle vibration, as seen in Fig. 1a, c and e. In Fig. 1b the second and third components were not much smaller than the first. However, in Fig. 1d and f the second component was considerably smaller than the first, but the third component was higher than the second. The three components found in the average EMGs in response to the vibratory burst do not necessarily imply that for each burst (out of the 50 that were applied per trial) the EMG had three components. To better understand these responses to the vibratory burst, Figs. 2 and 3 show the individual responses (each is drawn vertically displaced, from the bottom to the top) to each vibratory burst for the subjects associated with Fig. 1b and d, respectively. For the former subject, Fig. 2 shows clearly that three components, separated by about 10 ms,

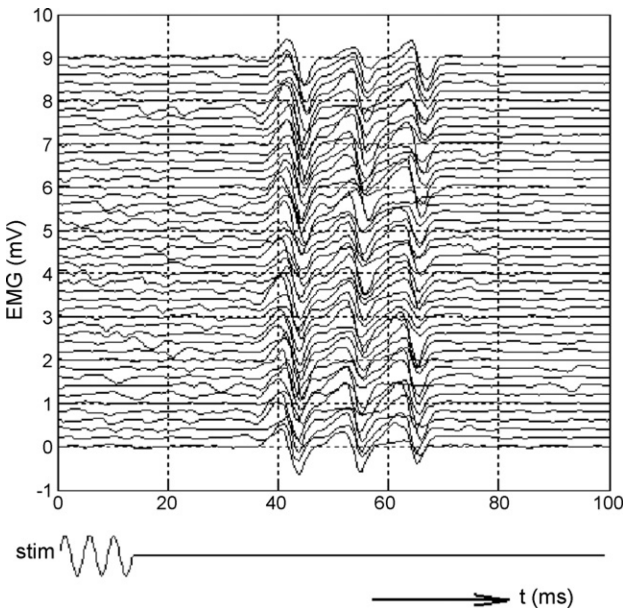

Fig. 2. Raw data corresponding to Fig. 1b, showing individual responses in the sequence (vertically displaced to allow visualization), ordered chronologically from the bottom to the top, in response to the vibratory burst applied at every 2 s.

occurred for every vibratory burst. However, for the latter subject, Fig. 3 shows that for the first few vibratory bursts there was a single component at the shortest latency. For later vibratory bursts there were components occurring about 10 ms and 20 ms after the first one, with more emphasis on the occurrence of the third component, which was also of higher amplitude.

A few of the subjects showed three components in their average EMGs in response to the vibratory burst even during quiet posture, while others had to lean forward and apply more load to the right leg. The latter subjects, when in quiet stance would respond with a single component, or more frequently, with two components

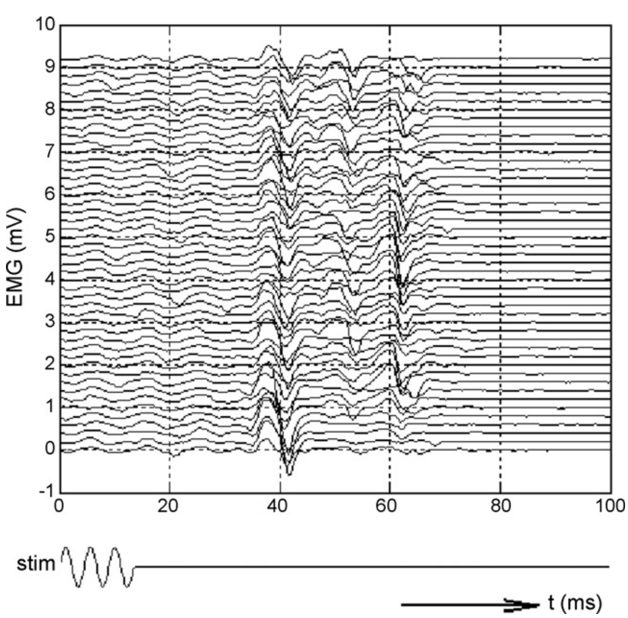

Fig. 3. Raw data corresponding to Fig. 1d, showing individual responses in the sequence (vertically displaced to allow visualization), ordered chronologically from the bottom to the top, in response to the vibratory burst applied at every 2 s.

in their average EMG, with either 10 ms or 20 ms of time interval between.

For the subjects exhibiting more than one EMG component per burst, a smaller vibratory amplitude could be found that made the second and third components disappear, there remaining the first component, with a much smaller amplitude than that found in response to the stronger vibration burst.

In all subjects the first EMG component amplitudes in response to the 50 bursts (applied at every 2 s) varied randomly around a mean value without any progressive increase in amplitude along time (e.g., Figs. 2 and 3).

A comparison of the figures at the left column of Fig. 1 with those at the right column suggests strongly that each component of the EMGs seen at the right is actually a reflex response and not part of a multi-phasic compound action potential. This means that each cycle of a given vibratory burst caused both an upstream volley through the Ia afferents and also a reflexively generated downstream volley through the motoneuron axons, which are then recorded as a muscle reflex. In some subjects under quiet stance, it was possible to obtain one reflex response per cycle of the vibratory burst, while in others this was only achieved when the subject was leaning forward towards the vibrated leg. The data in Fig. 1a, c and e discard the hypothesis that the second and third components in Fig. 1b, d and f are due to a polysynaptic action of the spindle group Ia afferents (or the spindle group II afferents) on the motoneuron pool. The existence of such pathways was elegantly shown in [28] for the wrist extensor muscles in humans using single motor unit recordings.

The experiments consisted of recording the soleus EMG of standing humans subjected to a brief, but powerful, sinusoidal Achilles tendon vibration. The results indicated that the reflex responses of the human motoneuron pool can respond to high frequency activation (100 Hz) from the Ia spindle afferents. The 2 s interval between subsequent vibratory bursts did not cause reflex depression, as seen by the amplitudes of the first response components along each trial (see Figs. 2 and 3). This is in accordance with previous results that showed that H reflexes generated in a contracting muscle showed no low-frequency depression [5]. The Ia afferent path from the muscle spindles up to the spinal cord seems able to follow 100 Hz vibrations, as both the spindles and axons can respond to such a frequency in a 1:1 fashion [6,22,26,27]. On the other hand, the soleus H reflex in humans is very sensitive to homosynaptic depression [19], as paralleled by the depression found in cat motoneuron EPSPs in response to successive activation of the Ia afferents [12]. However, a more refined analysis in cats has shown that the EPSP amplitude modulation depends on the type of motoneurons analyzed and on the frequency of the Ia spike train [21]: high threshold motoneurons (associated with fast motor units) were found to have synapses from the Ia afferents that do not depress or may even facilitate for high frequency stimulation. Data from humans have suggested that synapses from Ia afferents depress less in higher threshold motoneurons [14] and this may help explain the occurrence of two reflexes separated by only 10 ms (or 20 ms). Presynaptic inhibition caused by the vibration burst takes some time to build up and decays in a few hundreds of milliseconds [18], so it will not affect the EMG responses recorded at every 2 s. A simple interpretation of the results is that a first subset of motoneurons responded to the first cycle and a second subset, probably of higher threshold, responded to the second cycle. This second set of motoneurons had subthreshold EPSPs in response to the first afferent volley, which summed temporally to the (perhaps facilitated [21]) EPSPs induced by the next vibration cycle within the burst. A remaining hypothesis is that some motoneurons could be responding at 100 Hz, perhaps firing twice per burst, either to the first and second cycles or to the second and third cycles. This hypothesis cannot be tested with the present techniques, requiring needle electrode investigation of single motor unit activity. Most human motoneurons have been reported to respond with maximum firing rates below about 50 spikes/s, even though higher maximum firing rates have been described for some human motor units, usually from small size muscles [9,16] but also for the tibialis anterior [2,11]. It remains to be seen if soleus motor units are able to fire phasically with a 10 ms interspike interval.

The real picture is probably more complicated since other afferent types must also exert their influence in the generation of the response to the vibratory burst [4,13]. Muscle spindle secondary endings and Ib tendon afferents could be responding to the sinusoidal vibration, even if not in a 1:1 relationship with each cycle in a burst. In some cases, the Ib afferents may have contributed to the failure of reflex firings (mainly to the second and third cycles) to each cycle of the sinusoidal bursts, due to inhibitory effects on the homonymous motoneuron pool. The cutaneous effect of the tendon percussion by the tip of the shaker is a question that merits further investigation.

In conclusion, the results suggest that it is feasible to record high frequency reflex responses from human subjects, which allow examining different sets of motoneurons from the same pool and different spinal cord circuits. The combination of high frequency vibratory bursts with other techniques such as single motor unit recordings [32], hypoxia [10], mental computation [29], fatigue [3] should open new venues for research in human neurophysiology and also for clinical applications, such as in evaluations of spasticity [33], neuropathies and motor disorders. The standing position (with or without forward lean) seems to insure a sufficient descending drive to the motoneuron pool so that parts of it are always readily available to be discharged by the rapidly succeeding EPSPs that occur due to the muscle spindle group Ia afferent firings.

The data from the subjects did not indicate the existence of post-vibratory potentiation [21] as the reflex amplitudes did not increase with time along the 100 s of each experiment.

In the overall, these data have shown that, in many subjects, it is possible to record reflex responses at every 10 ms (or 20 ms), phase-locked to the cycles of a 100 Hz sinusoidal burst of vibration applied transversally to the tendon of the soleus muscle.

Acknowledgements

This research was funded by a grant from CNPq to the second author. The first author was a recipient of a fellowship from Capes. The technical assistance of Sandro A. Miqueleti is gratefully acknowledged.

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