Journal of Electromyography and Kinesiology 30 (2016) 249–262

Contents lists available at ScienceDirect

Journal of Electromyography and Kinesiology

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

Influence of timing variability between motor unit potentials on M-wave characteristics

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ARTICLE INFO

Article history:
Received 17 March 2016
Received in revised form 26 July 2016
Accepted 2 August 2016

Keywords:
Electromyogram
Motor unit potentials
Compound muscle action potential
M-wave potentiation
Conduction velocity

ABSTRACT

The transient enlargement of the compound muscle action potential (M wave) after a conditioning contraction is referred to as potentiation. It has been recently shown that the potentiation of the first and second phases of a monopolar M wave differed drastically; namely, the first phase remained largely unchanged, whereas the second phase underwent a marked enlargement and shortening. This dissimilar potentiation of the first and second phases has been suggested to be attributed to a transient increase in conduction velocity after the contraction. Here, we present a series of simulations to test if changes in the timing variability between motor unit potentials (MUPs) can be responsible for the unequal potentiation (and shortening) of the first and the second M-wave phases. We found that an increase in the mean motor unit conduction velocity resulted in a marked enlargement and narrowing of both the first and second M-wave phases. The enlargement of the first phase caused by a global increase in motor unit conduction velocities was apparent even for the electrode located over the innervation zone and became more pronounced with increasing distance to the innervation zone, whereas the potentiation of the second phase was largely independent of electrode position. Our simulations indicate that it is unlikely that an increase in motor unit conduction velocities (accompanied or not by changes in their distribution) could account for the experimental observation that only the second phase of a monopolar M wave, but not the first, is enlarged after a brief contraction. However, the combination of an increase in the motor unit conduction velocities and a spreading of the motor unit activation times could potentially explain the asymmetric potentiation of the M-wave phases.

1. Introduction

It is well known that the compound muscle action potential (M wave), as evoked by applying an electric stimulus to a peripheral nerve, increases after a brief muscle contraction. This phenomenon is normally referred to as ''M-wave potentiation'' and the underlying mechanisms are not entirely clear. One confounding factor in the study of M-wave potentiation is the fact that the contributions of the different motor units to the evoked compound potential are not perfectly aligned in time, but rather, they are dispersed due to a number of factors (see Fig. 1). Different motor unit properties influence the timing variability between MUPs, including differences in motor unit conduction velocities (CVs) (Dimitrova and Dimitrov, 2002), the spread of the distribution of these CVs (Keenan et al., 2006), and the spread of motor unit activation times (Rothwell et al., 1987; Magistris et al., 1998). This variability in the arrival times of motor unit potentials (MUPs) at the recording electrode can influence the size of the evoked monopolar M waves (Lee et al., 1975; Rhee et al., 1990; Stålberg and Karlsson, 2001; Farina et al., 2004). Therefore, it might be difficult to judge whether the increase in M-wave size after a brief contraction is due primarily to real physiological changes induced by the contraction, or due to changes in the timing between MUPs.

Although the most accepted mechanism for M-wave potentiation is enhancement of the electrogenic Na^{+}-K^{+} pump (Hicks and McComas, 1989), other explanations based on the synchronization between MUPs have also been put forward. In fact, the first explanation provided for the M-wave enlargement was a reduced dispersion in the activation times of muscle fiber action potentials after facilitation of neuromuscular transmission (Duchateau and Hainaut, 1985). More recently, an increase in conduction velocity has been recognized as a potential factor for the increase in M-wave size inasmuch as a global rise in motor unit CVs results in

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http://dx.doi.org/10.1016/j.jelekin.2016.08.003
1050-6411/

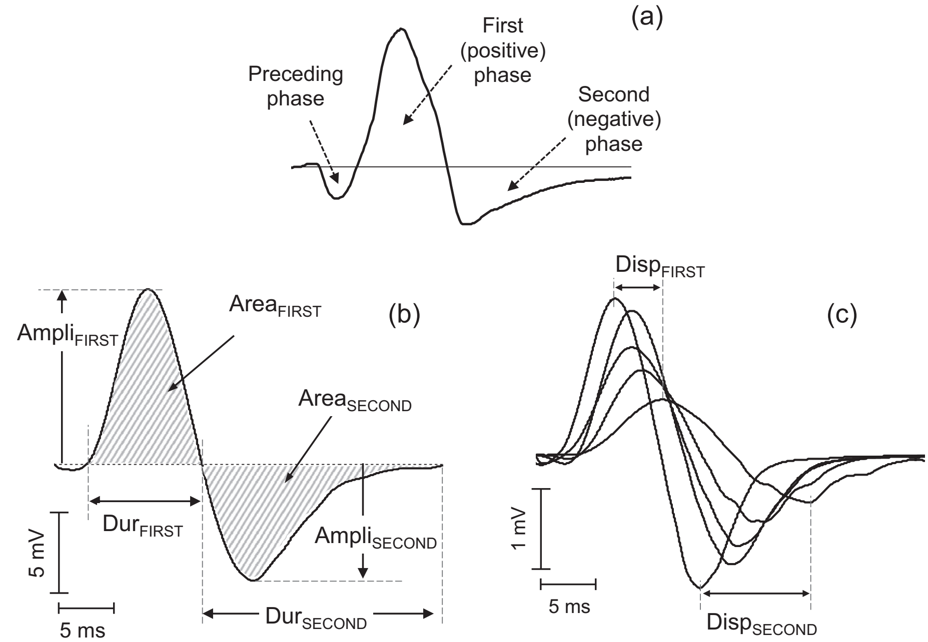

Fig. 1. (a) Definition of the first and second phases of the M wave according to the nomenclature used in the literature on M-wave potentiation. Note that an additional phase could appear preceding the two main ones when the belly electrode is placed away from the innervation zone. (b) Example of a simulated compound muscle action potential (M wave), and (c) five of its constituent motor unit potentials (MUPs). In plot (b), the amplitude, area, and duration of the first (Ampli$_{FIRST}$, Area$_{FIRST}$ and Dur$_{FIRST}$) and second (Ampli$_{SECOND}$, Area$_{SECOND}$ and Dur$_{SECOND}$) phases are indicated. In plot (c), the time dispersion between the first-positive peaks of the MUPs (Disp$_{FIRST}$), and between the second-negative peaks of the MUPs (Disp$_{SECOND}$) are shown.

a more synchronous (and hence efficient) summation of the electrical activity (Keenan et al., 2006). In this regard, there are now several reports based on surface EMG recordings suggesting that conduction velocity may increase transiently after a brief contraction (Van der Hoeven and Lange, 1994; Rutkove, 2000; Asawa et al., 2004). These findings seem to be in line with other experiments performed with needle electrodes indicating that an increase in conduction velocity occurs when a motor unit starts to fire after a short period of inactivity (Blijham et al., 2006; McGill and Lateva, 2011). Therefore, it might be that, when muscle fibers are stimulated after a conditioning contraction, their conduction velocity is elevated with respect to pre-contraction values (and the distribution of conduction velocities is also altered), thereby contributing to the enlargement of the evoked monopolar potential.

To clarify the involvement of the timing between MUPs in the phenomenon of M-wave potentiation it is essential to examine whether or not changes in this timing have differential effects on the first and second phases of the monopolar M wave. The reason is that, in a series of studies in the *tibialis anterior* and *quadriceps* muscles, we have shown that the potentiation of the first and second phases differed drastically (Rodriguez-Falces et al., 2015; Rodriguez-Falces and Place, 2016). Specifically, we found that, after brief conditioning contractions (shorter than 10 s), the amplitude of the M-wave first phase was not enlarged, whereas the second phase underwent a marked increase (see Fig. 2). Moreover, it was found that this unequal potentiation of the first and second phases was systematically accompanied by a pronounced decrease in the duration of the M wave, this reduction being more marked in the second phase (Fig. 2). Thus, the question arises whether a global increase in motor unit CVs (accompanied or not by other sources of variability in the timing between MUPs) can be responsible for the unequal potentiation of the M-wave phases and also for the M-wave shortening.

A clear understanding of how the timing between MUPs influences the first and second M-wave phases is of major importance for the interpretation of the phenomenon of M-wave potentiation. Addressing this question from an experimental point of view is difficult. An alternative strategy is to use computational models, as they afford the possibility of studying the effect of increases in motor unit CVs on the M-wave characteristics in isolation or in combination with changes in the spread of motor unit CVs and activation times. In addition, the use of simulations also permits to investigate how the distance from the electrode to the innervation zone influences the extent of potentiation in the first and second M-wave phases.

The objective of the present study was to use a simulation model of muscle evoked potentials to: (1) investigate the effects of changes in the timing variability between MUPs on the amplitude and duration of the first and second phases of an M wave, and (2) examine how these effects depend on the distance between the active electrode and the innervation zone. The study was undertaken to clarify if the asymmetric potentiation of the first and second phases of the monopolar M wave observed experimentally after a brief contraction can be explained by an increase in motor unit CV (with or without concurrent changes in the spread of motor unit CVs and activation times). The findings of the present study provide reference information that can be used to assist in the interpretation of potentiation-induced changes in monopolar M waves observed experimentally.

2. Material and methods

2.1. Experimental study

The present work used experimental signals recorded from the *biceps brachii* with which to test the predictions made with the analytical EMG model (see below). This model synthesized EMG signals in a fusiform muscle, in which action potentials propagate parallel to the skin surface. Therefore, we considered that the simulation results of this model are more accurately and reliably