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# Spike-triggered averaging provides inaccurate estimates of motor unit twitch properties under optimal conditions

Jakob L. Dideriksen[a,*], Francesco Negro[b]

[a] SMI, Department of Health Science and Technology, Aalborg University, Aalborg, Denmark
[b] Department of Clinical and Experimental Sciences, Università degli Studi di Brescia, Brescia, Italy

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ABSTRACT

Spike-triggered averaging is a commonly used technique for the estimation of motor unit twitches during voluntary contractions, although the obtained twitch estimates are known to be inaccurate in several conditions. Nevertheless, it is commonly assumed that a careful selection of the triggers may reduce the inaccuracy. This study aimed to analyze the impact of trigger selection criteria and thereby to identify the minimum estimation errors using a computational neuromuscular model. Force signals of five-minute duration were simulated at 10 contraction levels between 1 and 30% of the maximal voluntary contraction level (MVC) for motor unit pools of varying size (100, 300, and 800 motor units). Triggers were selected based on the inter-spike intervals (minimal value: 90–175 ms) and the number of triggers (minimal value: 100–800). The simulation results indicated that a minimum of 400 triggers with inter-spike intervals > 125 ms are needed to achieve the most accurate twitch estimates. Even under these conditions, however, a substantial estimation error remained (11.8–31.2% for different twitch parameters for simulations with 100 motor units). The error increased with the innervation number. The study demonstrates the fundamental inaccuracy of twitch estimates from spike-triggered averaging, which has important implications for our understanding of muscular adaptations.

## 1. Introduction

The output of the neuromuscular system is determined by the activity of the motor units and their contractile properties. For this reason, the pattern of motor unit action potentials (recruitment, rate coding) during voluntary contractions and the characteristics of the contractile response to action potentials (motor unit twitch) have been extensively studied. Examples of such studies include investigations of the effect of acute and chronic adaptations such as e.g. muscle fatigue (Carpentier et al., 2001), pain (Farina et al., 2008), and training (Van Cutsem et al., 1998) on these parameters. The discharge patterns of a subset of the active motor units can be identified in an unbiased way by decomposing intramuscular and/or surface electromyographic (EMG) signals (Marateb et al., 2011; McGill et al., 2005; Negro et al., 2016). Accurate estimates of the motor unit twitches during voluntary contractions, however, are more difficult to obtain. Typically, the twitch is estimated using spike-triggered averaging (STA), which involves averaging muscle force in short windows centered around the motor unit discharges (triggers) (Buchthal and Schmalbruch, 1970; Stein et al., 1972), enabling calculation of the twitch properties such as amplitude, contraction time and half relaxation time. The estimated twitch parameters from the STA technique, however, has been shown to be inaccurate in several conditions (Lim et al., 1995; Negro et al., 2014; Taylor et al., 2002).

There are two fundamental sources of errors in the twitch estimates from the STA. First, when the inter-spike intervals (ISI) of the trigger motor unit are sufficiently short, the consequent twitch summation may distort the twitch estimate. The phenomenon has been demonstrated experimentally by applying STA to the force evoked by electrically stimulated twitches of single motor axons at different frequencies (Calancie and Bawa, 1986; Thomas et al., 1990). Specifically, these studies found that increasing the frequency of action potentials implied an underestimation of the twitch properties. Accordingly, the length of the ISI before and after each trigger substantially impacts the twitch estimate during voluntary contractions (Gossen et al., 2003; Milner-Brown et al., 1973; Nordstrom et al., 1989). These observations have led to some studies imposing a minimum ISI (ISI-threshold; range: 100–150 ms) as inclusion criteria for triggers (Farina et al., 2008, 2005; Roatta et al., 2008; Van Cutsem et al., 1998). However, a recent investigation showed that this strict selection may even be detrimental for the estimation in some conditions (Negro et al., 2014). Second, the force produced by other motor units imposes noise on the estimate of

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* Corresponding author.
*E-mail address:* jldi@hst.aau.dk (J.L. Dideriksen).

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the target unit twitch. Under the assumption that the forces produced by different motor units are uncorrelated, a sufficient number of triggers should largely reduce this error. Moreover, a certain number of triggers is necessary to account for the natural short-term variability in the twitch shape (Celichowski et al., 2014). Consequently, most studies have imposed a lower limit for the number of triggers (trigger-threshold), but this limit varies largely across different study, e.g. < 50 (Carpentier et al., 2001; Stephens and Usherwood, 1977), a few hundreds (Farina et al., 2008, 2005; Milner-Brown et al., 1973; Van Cutsem et al., 1998), and > 1000 (Roatta et al., 2008; Semmler et al., 2000). The assumption of uncorrelated forces generated by different motor units, however, is violated when motor unit synchronization is present, which is usually the case during voluntary contractions (Keen et al., 2012). In general, high levels of motor unit synchronization impair accurate twitch estimation (Negro et al., 2014; Taylor et al., 2002).

Although the limitations of the STA technique have been well documented, many studies implicitly assume that STA is able to provide reliable estimates of twitch properties if the triggers are selected based on specific criteria. However, the appropriate values for the ISI- and number of trigger-thresholds as well as the relative magnitude of the errors in the estimated twitch properties that can be expected in the optimal case are unknown. In this study, we used a computational model to systematically investigate the quality of the estimates of twitch properties by STA obtained with different values of these thresholds and across a number of realistic conditions.

## 2. Methods

### 2.1. Simulations

The study adopted the model of motor unit activity and isometric force generation developed by (Fuglevand et al., 1993) with the distribution of minimum and peak discharge rates proposed by (Barry et al., 2007). As in other more recent applications of this model, the variability in the timing of the discharges was introduced by adding Gaussian noise to the motor neuron input (Dideriksen et al., 2012, Dideriksen et al., 2010). The magnitude of this noise was scaled to obtain a coefficient of variation for inter-spike intervals between 10% and 30% (Clamann, 1969; Moritz et al., 2005). The number of motor units in the model was set to 100, 300, or 800 representing the range of motor unit numbers for typical small and large muscles (Heckman and Enoka, 2004).

For each type of muscle, simulations were carried out with 10 different excitation levels (1, 2, 3, …,10), evoking a range of contraction levels below 30% of the maximum voluntary contraction level (MVC). Each simulation had a duration of 300 s. For each excitation level, simulations were carried out with or without a relation between twitch amplitude and contraction time. As in the original model, the relation between these parameters was modelled by a power function (Fuglevand et al., 1993).

### 2.2. Analysis

For each motor unit, the number of motor unit discharges for which the ISI were below the pre-assigned threshold (ISI-threshold) were excluded as suitable triggers. If the number of the included motor unit discharges was larger than the pre-assigned threshold of number of triggers (trigger-threshold), spike-triggered averaging was performed for the included motor unit twitch. The spike-triggered averaging involved selecting windows from the muscle force (duration: 600 ms), starting at the time of each trigger and calculating the average force across all windows. In this way, the average recurrent twitch waveform following each motor unit discharge was estimated. From each of these estimated motor unit twitches, the peak amplitude (maximum value in the first 150 ms), the contraction time (time to reach the maximum value in the first 150 ms) was calculated, and the half relaxation time (time from the peak amplitude to the twitch estimate has half that amplitude). In each simulation, spike-triggered averaging was performed with 18 different ISI-thresholds (90, 95, 100, …, 175 ms) and four different trigger-thresholds (100, 200, 400, 800). The trigger-threshold also served as the maximum number of motor unit discharges included, which implied that additional motor unit discharges that complied with the ISI-threshold were excluded once the trigger-threshold was reached. This procedure was implemented to ensure the consistency of the calculated results across simulations with different discharge properties.

The calculations described above were performed at each contraction level and resulted in a vector with the estimated twitch parameters for each individual motor unit that was included. If the same motor unit fulfilled the inclusion criteria in more than one contraction level, one estimate was randomly selected for further analysis. For each motor unit twitch estimation, the normalized rectified error of twitch amplitude, contraction time, and half relaxation time were calculated. Across the population of motor units, the two estimated parameters were log-log transformed (to linearize their relation) and linear regression was applied. This procedure was repeated 20 times to accommodate the random selection of parameters for motor units included in more than one contraction level. The average value for the normalized errors and correlation coefficients across the 20 repetitions were calculated.

## 3. Results

Fig. 1 shows an example of the output of the simulations with 300 motor units. Across the 10 simulations, the contraction level varied between 0.5% MVC and 29% MVC (Fig. 1A). The number of recruited motor units and their discharge rates increased at higher contraction levels (Fig. 1B). At the highest simulated contraction levels (> 20% MVC), all motor units were recruited, although the largest motor units were only active sporadically due to fluctuations in the synaptic noise (i.e. the average discharge rates were below their assigned minimum discharge rates). Fig. 1C shows the range of motor units for which at least 400 accepted triggers with ISI-thresholds above 110 ms occurred across the simulations. At the low contraction levels, only the smallest motor units could fulfil the criteria for inclusion. On the other hand, at higher force levels, the discharge rates of the same motor units were too high to allow 400 triggers within the ISI limits (> 110 ms). Using this combination of the two inclusion criteria (ISI-threshold: 110 ms; trigger-threshold: 400), almost all (293/300) motor units were included in the analysis for at least one of the 10 simulated contraction levels, while some motor units fulfilled the criteria at more than one contraction level. When the values for the two thresholds increased, however, the number of included motor units and the occurrence of motor units included at multiple simulations decreased.

Fig. 2 illustrates the process of spike-triggered averaging for one simulated motor unit (ISI-threshold: 110 ms). When the twitch estimate was derived from only a few triggers, substantial errors were observed for the three twitch properties (Fig. 2B–D). In this case, the estimates of twitch amplitude and contraction time tended to converge to a stable value at approximately 200 triggers. Whereas the estimates of twitch amplitude and half relaxation time underestimated those of the real twitch, the estimated contraction time converged to a near-correct value in this example.

Fig. 3 shows the actual and estimated motor unit twitch parameters (amplitude and contraction time) for all included motor units (ISI-threshold: 140 ms, trigger-threshold: 400) in simulations with 100 motor units. In this way, the figure contain estimates of twitch properties from simulations at all 10 contraction levels. Overall, the estimates are relatively accurate, as indicated by the average normalized rectified errors (twitch amplitude: 15.5%, contraction time 13.9%) and by the relation between the estimated amplitude and contraction time (similarity between grey and black line). The average error in half relaxation time (not shown), however, was 63.7%. Slow, low-amplitude