Comparison of fluctuations of motor unit recruitment and de-recruitment thresholds in man

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Received: 13 October 1992 / Accepted: 8 March 1993

Abstract. Recruitment and de-recruitment thresholds of motor units in the wrist extensor muscles can undergo important random fluctuations, even when they are measured during stereotyped contractions and relaxations. These fluctuations were statistically quantified and compared. The statistical analysis indicated that recruitment and de-recruitment thresholds display the same kind of fluctuations, and that the successive measurements are randomly distributed following a quasi-normal law. We suggest that the notion of force threshold for motor unit recruitment and de-recruitment might be oversimplified and that a motor unit seems to have a range of force in which it can be recruited or de-recruited. Comparison of the mean values of recruitment and de-recruitment thresholds of the motor units in the extensor carpi radialis muscles showed that de-recruitment thresholds were significantly lower than recruitment thresholds. This difference in the thresholds, together with the difference in the motor unit discharge frequency during a contraction and a relaxation, suggests a differential control of the motoneurone activity during contractions and relaxations.

Key words: Motor units – Recruitment threshold – De-recruitment threshold – Man

Introduction

In studies on the organisation of muscle contraction, the recruitment threshold of motor units, i.e. the level of overall force output at which firing onset occurs, is often taken into account. Motor unit recruitment threshold has been claimed to depend on the rate of the isometric contraction rise (Tanji and Kato 1973; Büdingen and Freund 1976), as well as on the sum of various afferent inputs to the motoneurone pool, such as cutaneous afferents (Garnett and Stephens 1980, 1981) or primary muscle spindle afferents (Grimby and Hannerz 1968, 1974). Variations in recruitment order, and therefore in recruitment threshold, have been reported. However, these variations, mainly observed in multifunctional muscles, are due to differences in the motor strategies (Person 1974; Thomas et al. 1978). Cases in which a reversal of motor unit recruitment order occurred during repetitions of the same task have been described for motor units recruited at very close levels of force (Tanji and Kato 1973). Yet, it is generally accepted that, under identical conditions, the recruitment threshold does not exhibit significant variations (Freund 1983; Denier van der Gon et al. 1985). However, in a previous study (Romaiguère et al. 1989a) we have shown that recruitment thresholds could undergo important fluctuations, even when studied under stereotyped conditions. This paper presents an attempt to statistically quantify these fluctuations, together with a comparison between recruitment and de-recruitment thresholds of the motor units in the wrist extensor muscles.

Materials and methods

Subjects and apparatus

Experiments were performed on 15 healthy human subjects, aged 20–30 years, with the approval of the local ethics committee (CCP-PRB–Marseille I, n°72/94). The subjects had given informed consent to the experimental procedure, as required by the Helsinki declaration (1964).

The subjects were seated in an adjustable armchair. Their left forearm was placed in a cushioned groove, so that a stereotyped position was maintained from one experiment to another. The distal end of the forearm was immobilised in a device leaving the wrist joint free and maintaining the hand in a semi-prone position, and 10° flexed. The hand was placed in a U-shaped device of adjustable width, which maintained the back of the hand in contact with an isometric force transducer calibrating the force of the muscle contraction in Newtons (N).

The subjects were seated in front of two oscilloscopes used to produce stimuli for the motor tasks by controlling the vertical displacement of the spots driven by the force transducer. A third oscilloscope, displaying motor unit activity and e.m.g of the wrist exten-
The e.m.g. of these muscles, and those of the extensor carpi radialis (0.25 N · s⁻¹), each one immediately followed by imposed-ramp contractions at 0.25 N · s⁻¹ while de-recruitment thresholds had been successively measured three to ten times, as well as to analyse the variability in de-recruitment thresholds, in order to become able to perform imposed-ramp contractions and relaxations (0.25 N · s⁻¹) during which motor unit force recruitment and de-recruitment thresholds were measured.

**Muscle activity recording**

Motor unit voluntary activation was studied on wrist extensor muscles, extensor carpi radialis longus and extensor carpi radialis brevis. The e.m.g. of these muscles, and those of the extensor carpi ulnaris and of the wrist flexor muscles were recorded simultaneously by means of paired surface electrodes 1.5 cm apart.

The subjects were first trained to perform selective contractions of the wrist extensor muscles by pushing on the force transducer device with the back of their hand. The retention device for the hand and forearm was designed so that it was easy to contract and relax these muscles without activating the wrist flexor muscles. The subjects quickly learned to keep their finger, arm and shoulder muscles relaxed during this task. The subjects were also trained to relax wrist extensor muscle contraction and relaxation to the vertical displacement of the oscilloscope spots driven by the force transducer, in order to become able to perform imposed-ramp contractions and relaxations (0.25 N · s⁻¹) during which motor unit force recruitment and de-recruitment thresholds were measured.

Recruitment thresholds were measured during voluntary imposed-ramp contractions at 0.25 N · s⁻¹ while de-recruitment thresholds were measured during voluntary imposed-ramp relaxations at −0.25 N · s⁻¹. To achieve these imposed rates, the subjects had to reproduce target lines drawn on the screen of the storage oscilloscope. Variability in recruitment thresholds was analysed from a first series of experiments concerning 84 motor units whose recruitment thresholds had been successively measured three to ten times, totalling 357 measures.

In order to compare recruitment and de-recruitment thresholds, as well as to analyse the variability in de-recruitment thresholds, in a second series of experiments, four of the fifteen subjects were asked to perform four to six (average five) imposed-ramp contractions (0.25 N · s⁻¹), each one immediately followed by an imposed-ramp relaxation (−0.25 N · s⁻¹, Fig. 1). Several motor units were recorded from each subject, so that 100 recruitment and de-recruitment threshold pairs were measured from 20 motor units.

In the two series of experiments, subjects were allowed to relax fully during 3 min before each trial. Experimentation never exceeded 3 h. Means and standard deviations of recruitment (first and second series) and de-recruitment thresholds (second series) were computed for each motor unit recorded.

**Results**

**Random fluctuations in motor unit recruitment threshold**

Figure 2A illustrates the results obtained in 27 motor units. As can be seen, most of the motor unit recruitment thresholds displayed an important variability during the experimental session.

In order to check whether the amplitude of the fluctuations was dependent on the mean recruitment threshold, the possibility of a statistical relationship between the mean and the standard deviation of each of the 84 motor units was investigated. Figure 3 shows that there is no obvious relationship between the two parameters. The slope of the best linear fit shows that the standard deviation slightly increased with the mean, but this estimation is not very accurate, as indicated by the low coefficient of linear correlation (r = 0.44). Nevertheless, Spearman's non-parametric test (performed on the non-weighted data) showed that the correlation between the mean and the standard deviation of recruitment thresholds is statistically significant (r = 0.56, P < 0.001). A similar analysis was performed when the means and standard deviations were weighted by the number of values used to calculate them, to minimise a possible sampling bias. In fact, this bias proved to be minimal since the correlation coefficient was only slightly changed (r = 0.46). The amplitude of the random fluctuations in the recruitment threshold of a motor unit tends thus slightly, but significantly, to increase with the mean.

An overall analysis of the distribution of the random fluctuations, including all the recruitment thresholds measured in this situation (for all the motor units pooled together), has been performed to accurately quantify the variability observed. This type of analysis is only interesting when it leads to the description of the pattern of recruitment threshold variability for a "standard motor unit". The distributions of the recruitment threshold measures of the various motor units should therefore be standardised, so that the overall distribution would reflect the most closely the individual distributions. The method used simply consisted in subtracting the mean of the recruitment threshold of a given motor unit from each measure of recruitment threshold of that unit. This kind of standardisation sets all the means to zero, but does not affect the standard deviation of the recruitment threshold of each motor unit. It is especially appropriate when the standard deviation of the recruitment threshold of each motor unit is independent of the mean, which is approximately the case: although the standard deviation tends slightly to increase with the mean (see Fig. 3), its value remains mostly unpredictable, since only 19% (= r²) of the variation of the standard deviation can be explained by the variation in the mean. This standardisation method was therefore better adapted to our case than any other one.

Figure 2B shows the distribution of recruitment threshold measures for all the motor units after standardisation. It is only slightly different from a normal distribution (Kolmogorov-Smirnov test: dₘₐₓ = 0.08, P < 0.05). Although the difference is statistically significant, the maximum distance (dₘₐₓ) between the theoretical and the observed distribution is small enough to suggest that the observed distribution is very close to a normal one. The significance of the difference can be explained by the high kurtosis of the observed distribution compared to that of a normal distribution (see Fig. 2B), but it is also possible that the lack of independence between the mean