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AN ELECTROMYOGRAPHIC STUDY ON THE FATIGUE OF SKELETAL MUSCLES IN CHICKENS

Noriji TABA*

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Abstract

Functional changes in the neuromuscular system associated with muscular fatigue were investigated in chickens by electromyographic observation. Alterations in discharge pattern on serial EMGs from the fatigued gastrocnemius and fibularis longus muscles were assessed in birds with prolonged forced extension of the hindleg joints. Discharges from a single NMU were also recorded and the serial intervals of discharge analyzed by the established procedures.

There was a uniform distribution of individual spike discharges immediately after start of sustained contraction of the muscle. With augmenting fatigue of the muscles, however, the discharges became gradually to group in clumps and eventually formed distinct grouping voltages.

Despite increasing muscular fatigue, the slow undulation of the discharge interval series from a single NMU remained consistently small in amplitude, showing a rather smooth course.

The r–S points determined from the irregular fluctuation of discharge interval series showed a remarkably narrow distribution of values immediately after initiation of the test and tended to expand progressively with enhancing fatigue of the muscles.

Introduction

Application of electromyography which provides information on states of functions of both the musculature and the underlying nervous system simultaneously is most effective as a measure to elucidate the mechanism of muscular fatigue since activities of skeletal muscles need to be investigated in association with activities of the motor nerves which supply the musculature. There have been several reports of observation of muscular fatigue by the application of electromyograms (EMG).

It was shown by Kondo3) that the discharge amplitude increased with fatigue as assessed by electromyography using surface electrodes. Emergence of grouping voltage in the EMG of fatigued muscles has been observed by Yamamoto11,12), by Yamada10) and by Kawamura et al13). Horiuchi15) described that fatigue of muscles brought about appearance of grouping voltage and undulation of the discharge interval. In a previous report6,7) from this laboratory, it was demonstrated by analysis of the discharge interval series from a single neuromuscular unit (NMU) that functional impairment of the regulatory system occurs at the spinal level and the motor areas of the cerebral cortex project enhanced influences when skeletal muscles are in a state of fatigue.

These studies, nevertheless, are concerned with muscular fatigue in man and other mammals with particularly well developed motor systems while reports of investigation on the mechanism of muscular fatigue in the aves with morphologically undeveloped cerebral cortex in which activities of the skeletal muscles are generally thought to be totally controlled via the extrapyramidal tracts as yet are few. This study was undertaken to investigate the time-course of changes in function of the neuromuscular system associated with fatigue in chickens by analysis of discharge interval series from single

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NMUs in the muscles fatigued by forced extension of hindleg joints.

Materials and Methods

Six normal cockerels, about 4 months of age, were used in the experiments.

The gastrocnemius muscle and fibularis longus muscle from which stable action potentials can be most readily led off among other muscles of the hindleg were subjected to the test. Muscular fatigue was evoked by continuous contraction of these muscles with forced extension of hindleg joints over a long period.

The gastrocnemius muscle was contracted by suspending the right leg with a weight hanged on its metatarsus, whereas contraction of the fibularis longus muscle was achieved by forced extension of the knee and ankle joints of the left leg with the bird restrained in lateral position on a board. By these procedures both muscles were maintained in a state of marked contraction so that the bird appeared incapable of standing in normal upright posture immediately after completion of the test.

EMGs of each muscle were recorded on six occasions during contraction, namely, immediately and at 10, 30, 60, 90 and 120 minutes after start of experiment. By use of coaxial needle electrodes for clinical use were action potentials from many NMUs led off onto a Braun tube oscillograph, and the potential changes displayed on its fluorescent screen were photographically recorded. Immediately following it, discharges from a single NMU were separately led off and continuously recorded with an electromagnetic oscillograph.

From discharge intervals of a single NMU determined from the EMG patterns thus obtained, a discharge interval diagram was made. From the diagram, slow undulations and irregular fluctuations were extracted by the usual technique. A $t$-$S$ correlation diagram was then prepared by plotting the mean discharge interval ($t$) calculated from the discharge interval series against the standard deviation ($S$) obtained from the irregular fluctuations.

Results and Discussion

1. EMG Patterns

The joints of the leg of bird were extended by compulsion over approximately 2 hours in order to cause fatigue of the test muscles in a short period. Both the genual and pedal articulations were extremely extended with a sustained marked contraction of the test muscles under this condition. When maintained over a long period in such state, the bird made gestures of impatience and pain, moving vigorously its head, neck and forelimbs. After about 30 minutes in that posture, the bird developed intermittent trembles in the knee joint. As this condition was interpretable as representing a consequence of muscular fatigue, EMGs were recorded from the muscles to detect and analyze potential changes.

Figure 1 (A) is an EMG obtained from the fibularis longus muscle immediately after start of the test; a pattern of normal interference voltage with virtually uniformly distributed spike discharges is seen. Shown in Figure 1 (B) is an EMG recorded 10 minutes after initiation of the test. Discharges are dense in some time segments and rather sparse in others; yet the discharge pattern is still remote from what is called grouping voltage. After 30 minutes had elapsed following start of the test, muscular trembling was palpable even through feathers, indicating that the bird was in a state of considerably profound fatigue. The EMG showed fairly rhythmically grouped multiple spikes; hence a pattern of so-called grouping voltage (Fig. 1 (C)). From this period on, the EMG displayed consistently a distinct pattern of grouping voltage throughout till even after 120 minutes of sustained muscular contraction (Fig. 1 (D), (E), (F)).

Figure 1 (A') shows an EMG recorded from the gastrocnemius muscle immediately after initiation of the test. The pattern is that of characteristically normal interference voltage as seen with the fibularis longus muscle. Presented in Figure 1 (B') is an EMG obtained at 10 minutes of sustained muscular contraction; the discharge already has a distinct feature of grouping voltage, thus unlike the case of the fibularis longus muscle. However, no muscular
Fatigue of skeletal muscles in chickens

Fig. 1. EMG patterns of the fibularis longus muscle and the gastrocnemius muscle recorded in process of time under continuous contraction in the fowl.

Trembling could be palpated yet at this stage, the muscle appearing not noticeably fatigued. Thirty minutes after start of the test trembles of the muscle appeared, indicating that the bird grew considerably wearied. The EMG had a typical grouping voltage pattern at this stage (Fig. 1 (C')). Subsequent series of tracings obtained 60, 90 and 120 minutes of sustained contraction showed consistent patterns of grouping voltage [Fig. 1(D'), (E'), (F')].

Spike discharges recorded from a plurality of NMUs of a normal muscle contracted in a constant intensity had a virtually uniform distribution of individual spikes, with few or no sparse segments in the EMG. As the muscle got fatigued due to sustained contraction, the discharge intervals of spikes became gradually irregular, eventually making the spike discharge grouped in clumps with development of muscular trembles. The grouping voltage is an EMG abnormality and the mechanism whereby it occurs has not been fully elucidated despite numerous studies. Diminution in afferent impulses has been implicated, besides dysfunction of the central motor nerve system, in the genesis of grouping voltage.

In a previous study, the author made observation of changes in EMG pattern of canine hind-leg muscles under continuous contraction with the finding of a gradual grouping of discharges in association with muscular fatigue, which might be attributed to diminution in afferent impulse due to hypofunction of the muscular self-receptors. The present experiment similarly demonstrated a gradual alteration in EMG pattern to distinct grouping voltage with sustained muscular contraction in birds. The behavior of birds undergoing the test and their incapability of standing in normal upright posture immediately after the test would indicate ascribability of the grouping voltage to muscular fatigue, possibly consequent to diminution of afferent impulses from the muscular self-receptors.

2. Discharge Intervals of a Single NMU

Grouping voltage emerge in the EMG with long-sustained contraction of the muscle as described above. On the assumption that some particular alteration might occur in the pattern of discharge from a single NMU following onset of fatigue, provided the afferent impulse play an important role in the development of grouping voltage, discharge interval series of a single NMU were statistically analyzed. Serial discharge intervals of a single NMU incessantly vary and do not show a constant magnitude at any time even despite an attempt of maintaining muscular contraction at a constant level, as have been reported in the literature. The variation of discharge interval series of a single NMU has been described to be comprised usually of two types of variations, i.e. a slow undulation and an irregular fluctuation. In view of this, experiments were performed to extract these two types of variations from the discharge interval series and analyze them respectively.
(1) Slow undulation

Slow undulation was isolated from the discharge interval series by eliminating irregular fluctuation by the arithmetic moving average method. In Figure 2, most frequently appearing patterns of slow undulation from respective test muscles seen immediately and at 10, 30, 60, 90 and 120 minutes after start of the test are shown, one example each, with the mean discharge interval as a base line.

In both test muscles the slow undulation immediately after start of the test was characterized by a smooth course of curves with remarkably narrow amplitudes, thus indicating stable discharge activity at this stage. Essentially the same pattern of slow undulation as that seen immediately after the test was observed at 10 minutes of sustained contraction; it had a remarkably stable course with narrow amplitudes. However, after 30 minutes had elapsed following initiation of the test the amplitude became somewhat increased and small waves emerged in modest quantities. The course of curves itself appeared still generally smooth. This state continued thereafter and the curves remained stable even after 120 minutes of sustained contraction.

Inasmuch as slow undulation is a series of running means and therefore is indicative of the average progress of discharge intervals of a single NMU, the state of activity of an NMU can be generally viewed from its amplitude and regularity. On detailed analytical assessments of slow undulations obtained from muscles of the lower extremities of normal men, decerebrated cats, patients with parkinsonism or tabes dorsalis and those with cerebellar ataxia, Nomura (4-5) has noted that the slow undulation reflects a continuous alteration in the degree of activity of the higher motor nerve system which designates the muscular activity and that afferent impulses have close bearing on determination of the pattern and magnitude of undulation. The present author observed in the previous study in dogs a progressive increase in amplitude of slow undulation with augmenting fatigue of the hindlimb muscle, along with frequent appearance of irregular grand undulations, which phenomenon was interpreted as representing an increase in undulation of activity of the higher motor nerve system arising from muscular fatigue.

In the present investigation, nevertheless, the
Fig. 3. Correlation diagrams between average and standard deviation of discharge intervals of the fibularis longus muscle and the gastrocnemius muscle in the fowl.
slow undulation failed to show any conspicuous change in amplitude even at the stage with a distinct grouping voltage in the EMG indicating fatiguedness of the muscle. This finding suggests that the higher nervous system might continue to retain its stable activity despite development of muscular fatigue in chickens which are anatomically devoid of the pyramidal tract.

(2) Irregular fluctuation

After elimination of the slow undulation from the discharge interval series, the irregular fluctuation remains. The standard deviation (S) was calculated from this series and the mean discharge interval (\( \tau \)) from the original discharge interval series, respectively. A \( \tau - S \) correlation diagram was prepared for each muscle by plotting S as ordinate against \( \tau \) as abscissa (Fig. 3).

In the case of the fibularis longus muscle, the diagram from the data obtained immediately after start of the test showed a dense distribution of points generally with only a slight dispersion, thus indicating a relatively stable muscular activity. As a discharge pattern with a tendency to grouping appeared in the EMG at 10 minutes of sustained contraction, the distribution of \( \tau - S \) points became largely biased to the right and widened. This tendency became more pronounced after 30 minutes of sustained contraction as distinct grouping voltage occurred and particularly conspicuous after 120 minutes.

A straight line (\( \tau - S \) curve) representing the interrelationship of \( \tau \) and S was drawn in each \( \tau - S \) correlation diagram, and the \( \tau - S \) curves from the serial diagrams at the consecutive periods after initiation of forced persistent muscular contraction were collected in a fashion that they intersected each other at one point for convenience of comparing their gradients (Fig. 4). As can be seen from Figure 4, it is obvious that the gradient of the \( \tau - S \) curve increased progressively with time, suggesting that muscular fatigue gave rise to a gradual increase in the amplitude of variations in discharge interval.

With the gastrocnemius muscle, \( \tau - S \) points immediately after start of the test were densely gathered in the lower part of the diagram though in a somewhat greater confines of distribution than the case of the fibularis longus muscle.

The confines of distribution remained essentially the same at 10 minutes of sustained contraction, that is to say, there was little or no prolongation of discharge intervals or increase in their variation amplitude. After the lapse of the first 30 minutes the range of distribution began conspicuously expanding, and this trend became moreover marked after 60 minutes following start of the test. A progressive increase of gradient of the \( \tau - S \) curve with time was evident as was the case of the fibularis longus muscle (Fig. 4). Thus, discharge intervals of the gastrocnemius muscle also displayed a progressive increase in amplitude of variation with augmenting fatigue of the muscle.

It is generally recognized that \( \tau - S \) points determined from the discharge interval series of a single NMU are distributed along a curve (\( \tau - S \) curve) which is comprised of two parts, a
horizontal course and a course prone to ascending. The points along the former have been interpreted as belonging to NMUs under the control of cerebral subcortical nervous system whereas those along the latter to NMUs under the control of the nervous system of the cerebral cortical motor area. However, it has been shown by Nomura that the r-S curve is virtually linear as a whole in cases of animals with phylogenetically undeveloped pyramidal tracts such as the chicken, rabbit and goat, in which the amplitude of variation increases proportionately with increasing interval of discharges. The investigator has described accordingly that the activity of skeletal muscles is affected by that of nervous systems other than the motor area of the cerebral cortex in these animals.

In the present study, it was found that the r-S points tended to be distributed along a straight line of which the gradient increased progressively on sustained contraction of the muscle. It follows that the amplitude of variations in discharge interval of a single NMU increases with enhancing fatigue of the muscle.

Contractile activity of muscles is considered to be not solely effected by the activity of the higher nervous system but constantly modulated via function of the autoregulatory system of the spinal cord driven by afferent impulses from peripheral receptors. The dense gathering of points in the lower part of the r-S correlation diagram with a small gradient of the r-S curve immediately after start of the test appears to reflect a possible minimization of the amplitude of variations in discharge interval by smooth operation of this regulatory mechanism. It would be reasonable to assume in this connection that some abnormality occurs in the regulatory mechanism on sustained contraction of the muscle, probably due to diminution in afferent impulses from muscular self-receptors, leading to an increase in the amplitude of variations in discharge interval. As described in the report from this laboratory, similar gradual increments of the amplitude of discharge interval changes in a single NMU of fatigued muscle were observed in dogs. The increase in variation amplitude seen in chickens, nevertheless, was less conspicuous than in dogs. This disparity would be attributable to the muscular activity being mostly effected by the function of the cerebral subcortical nervous system in chickens with the phylogenetically undeveloped pyramidal tracts.

References

ニフトリにおける骨格筋疲労の筋電図学的検討

田場 典 治

要 約

1. ニフトリを用いて、筋疲労時における神経一筋系の機能的変化を筋電図学的に検討した。後肢関節の長時間伸展により、M. gastrocnemius および M. fibularis longus を疲労させ、これらの筋から筋電図を経時的に記録し、その放電パターンの変化を検討した。また、单一NMUの放電を記録し、その放電間際を方式に従って解析した。

2. 個々の spike 放電は、実験開始直後は均等に分布しているが、筋疲労の進行とともに次第に群化し、ついには明瞭な grouping Voltage を形成した。

3. 単一NMUの放電間隔時系列の緩慢な変動は、筋疲労の発現にもかかわらず、帯状変動幅が小さく、その経過は滑らかであった。これより、上位運動神経系は、筋疲労時においても比較的安定した活動を続けているものと解釈した。

4. 不規則な変動の変動幅は、実験開始直後は極めて小さいが、筋疲労の進行とともに次第に増大する傾向を示した。これを筋疲労に伴う下位運動神経系の機能減退と考えた。