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Quantitative evaluation of post-stroke upper limb spasticity based on multi-parameter surface electromyography signal analysis

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Abstract

Purpose: This study aims to explore the application value of multi-parameter surface electromyography (sEMG) combined with Motor Status Scale (MSS) score in the evaluation of post-stroke upper limb spasticity.

Methods: 42 patients with post-stroke upper limb spasticity were enrolled in a self-controlled study design. All patients received routine neurological treatment and rehabilitation training. The iEMG, root mean square (RMS) value, median frequency (MF), and mean power frequency (MPF) were analyzed, and the co-contraction ratio (CR) was calculated.

Results: After treatment, the iEMG, RMS, MF, and MPF values of the forearm flexor and extensor muscle groups significantly increased in the 42 patients ($P<0.05$). At rest, the RMS and iEMG values of the affected forearm flexor and extensor muscles were significantly higher than those of the unaffected side and the healthy control group ($P<0.05$). During active movement, the RMS and iEMG values of the affected muscles were significantly lower than those of the unaffected side and the healthy control group ($P<0.05$). The total MSS score was significantly increased compared with that before treatment ($P<0.001$). sEMG parameters were negatively correlated with balance function parameters ($P<0.05$). The modified Ashworth Scale assessment showed that the total effective rate was 95.24%. Receiver operating characteristic curve analysis revealed that the AUC values of iEMG, RMS, MF, and MPF for evaluating the efficacy were 0.748, 0.731, 0.737, and 0.826, respectively ($P<0.05$).

Conclusion: Multi-parameter sEMG analysis combined with MSS score can objectively and quantitatively evaluate the functional status of post-stroke upper limb spasticity.

Keywords: stroke; upper limb spasticity; surface electromyography; Motor Status Scale; functional evaluation

1 Introduction

Stroke is a common cerebrovascular disease that poses a serious threat to human health, with more than 13 million new cases reported worldwide each year [1]. According to the 2018 China Stroke Prevention and Treatment Report, the number of stroke patients in China has exceeded 10 million, and the incidence rate continues to rise annually [2]. With advances in medical technology, the mortality rate of stroke has declined significantly, but the disability rate remains high, making it the leading cause of disability in adults [3]. Upper limb spasticity is a common motor dysfunction after stroke, with an incidence of approximately 40%. Due to the larger projection area of the upper limbs in the motor cortex of the brain, the incidence of spasticity in the upper limbs is significantly higher than that in the lower limbs [4]. Spasticity severely affects patients' ability to perform daily activities, resulting in limitations in basic life skills such as dressing and eating, and it may also cause complications such as pain, sleep disorders, and joint contractures, seriously impairing patients' quality of life and mental health [5].

Currently, the clinical assessment of spasticity mainly relies on subjective evaluation methods such as the modified Ashworth Scale (MAS), which has limitations such as large inter-rater differences and low sensitivity [6]. Surface electromyography (sEMG), as a non-invasive neuromuscular function detection technology, can record muscle electrical activity in real time and provide objective and quantitative evaluation indicators [7]. In recent years, the application of sEMG in stroke rehabilitation assessment has gradually gained attention, especially through the analysis of multiple parameters such as iEMG, root mean square (RMS), median frequency (MF), mean power frequency (MPF), etc., which can comprehensively reflect muscle contraction characteristics, nerve conduction velocity, and motor unit status [8]. The Motor Status Scale (MSS) is specifically designed for the assessment of upper limb function in stroke patients. Compared with the traditional Fugl-Meyer assessment, the MSS has higher sensitivity and more comprehensive assessment dimensions, especially more detailed assessment of fine hand movements [9]. However, the use of MSS alone still has the issues of subjectivity, making it difficult to accurately quantify muscle function status.

Therefore, the aim of this study was to explore the application value of multi-parameter sEMG analysis combined with MSS score in the evaluation of post-stroke upper limb spasticity, thereby providing a more objective and accurate evaluation tool for clinicians and guiding the formulation of individualized rehabilitation treatment plans.

2 Materials and Methods

2.1 Study design

This study used a prospective, self-controlled design and was conducted in the Department of Neuroelectrophysiology of Beijing Jishuitan Hospital, Capital Medical University from July 2024 to June 2025. The study protocol was approved by the ethics committee of Beijing Jishuitan Hospital, Capital Medical University, and all patients provided signed informed consent.

2.2 Study subjects

2.2.1 Inclusion criteria

(1) Diagnosis of ischemic stroke according to the Chinese Guidelines for Diagnosis and Treatment of Acute Ischemic Stroke (2023) [10] or diagnosis of hemorrhagic stroke according to the Chinese Guidelines for Diagnosis and Treatment of Cerebral Hemorrhage (2019) [11]; (2) Determination of responsible lesion by cranial CT or MRI scan; (3) Age 18−70 years; (4) First-time onset, with MAS grades I–III in the affected limb; (5) Unilateral limb involvement, with disease duration <6 months; (6) Clear consciousness and able to cooperate with treatment.

2.2.2 Exclusion criteria

(1) Limb spasticity caused by other diseases such as craniocerebral trauma, tumors, and inflammation; (2) History of cranial surgery; (3) Impaired consciousness, aphasia, or unstable vital signs; (4) Concurrent severe cardiac, hepatic, or renal dysfunction, hematologic disorders, or psychiatric disorders; (5) Prior use of muscle relaxants or botulinum toxin injections after the onset of the disease; (6) Pre-existing limb lesions; (7) Fear of acupuncture or needle syncope; (8) Presence of hemispatial neglect

syndrome.

2.3 Intervention measures

All patients received routine neurological treatment, including blood pressure control, glycemic and lipid regulation, antiplatelet aggregation, and neurotrophic measures. They also received standardized rehabilitation training, including range of motion training, muscle strength training, and coordination exercises, once daily for 45 minutes each session, with the treatment lasting for 12 weeks.

2.4 Observation indicators and detection methods

2.4.1 sEMG testing

An eight-channel Keypoint EMG system (Dantec, Denmark) with customized forearm electrode patches was used to synchronously record the sEMG signals of target forearm muscles. Before testing, the skin was cleaned with 75% ethanol. Electrodes were positioned on the anterior and posterior surfaces of the forearm. The anterior forearm recordings included the flexor pollicis longus, flexor digitorum superficialis, flexor carpi ulnaris, flexor carpi radialis, and pronator teres. The posterior forearm recordings included the extensor digitorum, extensor carpi radialis, and extensor pollicis longus. The sampling frequency was set at 2000 Hz, with a 20-500 Hz bandpass filter. Electrode placement was performed in accordance with the Surface ElectroMyoGraphy for the Non-Invasive Assessment of Muscles (SENIAM) guidelines. The specific electrode positions are shown in **Appendix 1**. The electrodes were aligned with the direction of the muscle fibers, with an inter-electrode distance of 20 mm. The reference electrode was placed over the ipsilateral olecranon of the ulna, serving as a bony landmark. Electromyography (EMG) acquisition and MSS scoring were performed within the same examination session (on the same morning, with an interval of no more than 2 hours) to ensure temporal consistency between the two assessments. Each evaluation was conducted independently by two trained assessors, who were blinded to each other's results.

Data processing: Through Fast Fourier Transform (FFT) analysis, the following parameters were extracted: (1) iEMG, which reflects muscle contraction intensity; (2) RMS, which reflects the change in electromyographic amplitude; (3) MF, which reflects the composition of muscle fiber types; (4) MPF, which reflects the conduction velocity of motor units. The co-contraction ratio (CR) was calculated as: CR = [Antagonist RMS / (Agonist RMS + Antagonist RMS)] × 100%.

2.4.2 MSS scoring

The MSS upper limb assessment included five dimensions and 29 items: shoulder movement (20 points), elbow and forearm movement (18 points), wrist movement (14 points), hand movement (20 points), and upper limb movement based on hand function (10 points), with a total score of 82 points [9]. Scoring was performed by trained rehabilitation therapists, with higher scores indicating better function. Detailed descriptions of the assessment dimensions are shown in **Appendix 2**.

2.4.3 Balance function testing

The Balance system SD (Biodex, USA) was used for dynamic and static balance testing. The patient stood barefoot with feet together on the testing platform, looking straight ahead. This position was maintained for 30 seconds. The length (cm) of the center of gravity trajectory and the envelope area (cm^2) were recorded. In this study, the balance test was performed once per assessment under eyes-open conditions. In this study, a feet-together standing posture was adopted, which differs from the standard posture recommended by the Biodex Balance System (feet slightly apart and externally rotated). This approach was chosen to ensure consistency with the postural requirements of certain standing upper-limb functional assessment items in the MSS scale, thereby facilitating the comparison of the association between upper-limb electromyographic parameters and balance function under similar conditions.

2.4.4 Efficacy assessment

According to the changes in the MAS, efficacy was assessed. A reduction of grade 0 was considered complete recovery; a reduction of ≥2 grades but not reaching grade 0 was considered marked improvement; a reduction of 1 grade but not reaching grade 0 was considered improvement; and no change was considered ineffective. The total effective rate = (complete recovery + markedly effective + effective) / total number of cases × 100%.

2.5 Sample size calculation

Based on the pilot study results, with α = 0.05, β = 0.20, and an effect size d = 0.5, the paired t-test sample size calculation formula was applied. Accounting for a 10% dropout rate, the sample size was determined to be 42 participants.

2.6 Statistical methods

Data analysis was performed using SPSS 26.0 and GraphPad Prism 9.0. Continuous data were expressed as mean ± standard deviation, and paired t-tests were used for comparison before and after treatment. Categorical data were presented as number of cases and percentages. Correlation analysis was performed using the Spearman's correlation coefficient. Receiver-operating characteristic (ROC) curves were used to analyze diagnostic performance, and the area under the curve (AUC), sensitivity, and specificity were calculated. $P<0.05$ was considered statistically significant.

3 Results

3.1 Analysis of patient baseline data

The mean age of the 42 patients was 52.45 years, and 57.14% were male. The mean disease duration was 3.28 months. Ischemic stroke constituted 66.67% of cases. The majority (42.86%) was grade II according to the MAS (**Table 1**).

Table 1 Baseline data of 42 patients with post-stroke upper limb spasticity

Clinical characteristics	Value/number	Percentage (%)
Age (years)	52.45±8.76	-
Sex (male/female)	24/18	57.14/42.86
Disease duration (months)	3.28±1.45	-
Ischemic stroke	28	66.67
Hemorrhagic stroke	14	33.33
Modified Ashworth Scale grade I	12	28.57
Modified Ashworth Scale grade II	18	42.86
Modified Ashworth Scale grade III	12	28.57

3.2 Comparison of sEMG parameters of forearm muscles at rest

At rest, the RMS and iEMG values of the affected forearm flexor and extensor muscles were significantly higher than those of the unaffected side and the healthy control group (P<0.05), indicating abnormal muscle electrical activity in the spastic limb even during rest. The abnormality was more pronounced in the anterior forearm flexor muscles, which is consistent with the typical flexor spasticity pattern observed after stroke (**Table 2**).

Table 2 Comparison of electromyographic amplitude parameters of various muscles between patients and normal participants at rest

Group	Anterior forearm flexor muscles (RMS/iEMG)					Posterior forearm extensor muscles		
	Flexor pollicis longus	Flexor digitorum superficialis	Flexor carpi ulnaris	Flexor carpi radialis	Pronator teres	Extensor digitorum	Extensor carpi radialis	Extensor pollicis longus
Affected side	47.1/37.1	45.6/35.9	40.0/31.0	33.2/25.8	36.5/28.4	41.7/33.1	26.4/20.3	24.8/19.1
Unaffected side	8.6/6.7	8.7/6.9	9.3/7.3	8.8/6.9	8.5/6.6	10.8/8.6	18.0/12.6	15.3/11.8
Healthy control	12.5/9.6	8.7/6.5	5.8/4.6	5.7/4.6	6.4/5.1	9.3/7.4	6.2/5.0	5.6/4.5

Note: RMS is expressed in μV, and iEMG is expressed in μV·s.

3.3 Comparison of sEMG parameters of forearm muscles during active movement

During active movement, the RMS and iEMG values of the affected forearm muscles were significantly lower than those of the unaffected side and the healthy control group (P<0.05), indicating reduced muscle activation capacity during active contraction in the spastic limb. In contrast to the resting state, functional impairment was more pronounced in the extensor muscles during active movement (**Table 3**).

Table 3 Comparison of sEMG parameters of forearm muscles during active movement

Group	Anterior forearm flexor muscles (RMS/iEMG)					Posterior forearm extensor muscles		
	Flexor pollicis longus	Flexor digitorum superficialis	Flexor carpi ulnaris	Flexor carpi radialis	Pronator teres	Extensor digitorum	Extensor carpi radialis	Extensor pollicis longus
Affected side	123.1/93.0	117.9/88.9	79.5/60.2	74.5/57.7	82.6/63.1	68.1/53.3	128.7/99.8	58.4/45.6
Unaffected side	180.1/133.2	184.4/134.2	202.5/148.0	160.3/118.6	175.8/129.5	111.7/78.6	177.2/126.8	98.5/72.8
Healthy control	318.8/220.6	375.2/245.0	464.1/325.7	254.9/182.2	287.3/201.5	193.8/140.6	269.5/180.9	178.6/128.3

Note: RMS is expressed in μV, and iEMG is expressed in μV·s.

3.4 Comparison of MSS scores in enrolled patients before and after treatment

The MSS scores across all dimensions of enrolled patients increased significantly after treatment compared to before treatment (P<0.05). The total MSS score of enrolled patients was (31.75 ± 8.76) before treatment and (55.63 ± 10.42) after treatment (t = 26.617, P<0.001) (**Figure 1**).

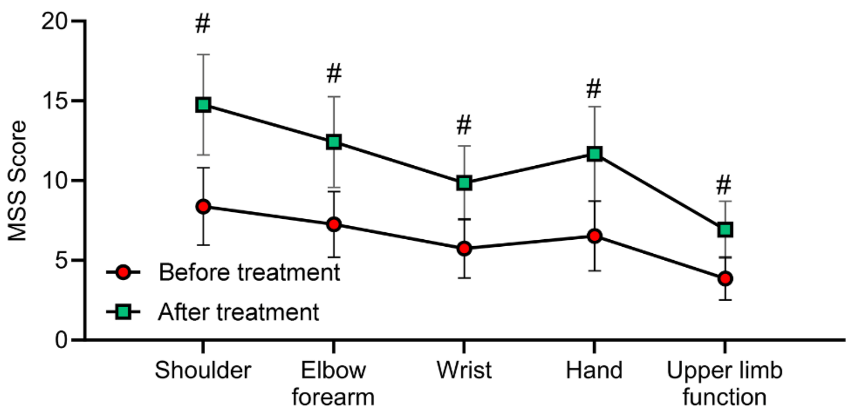

Figure 1 Comparison of MSS scores in enrolled patients before and after treatment

3.5 Correlation analysis between sEMG signals and balance function parameters

The balance function of patients was assessed using a balance testing system before treatment. Two parameters, including trajectory length and envelope area, were collected. Spearman correlation was analyzed between the trajectory length and envelope area and the neuromuscular function of the affected forearm flexor muscles in the enrolled patients. Results indicated that the EMG parameters of enrolled patients showed negative correlations with both trajectory length (**Figure 2**) and envelope area (**Figure 3**) (P<0.05) (**Table 4**).

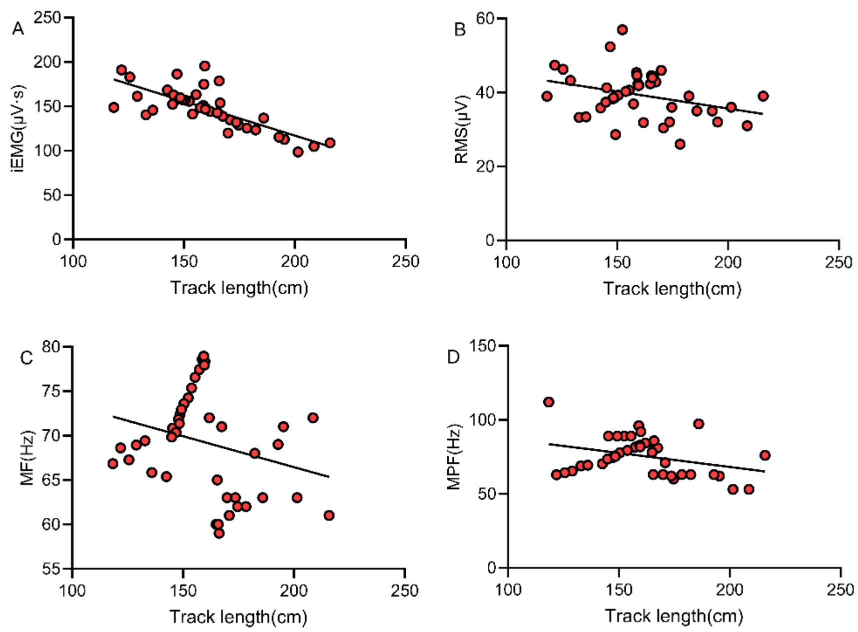

Figure 2 Correlation analysis between trajectory length and EMG parameters

The trajectory length was negatively correlated with iEMG (figure A), RMS (figure B), MF (figure C), and MPF (figure D) (P<0.05). Note: Neuromuscular function was represented by the mean values of iEMG, RMS, MF, and MPF derived from the flexor pollicis longus, flexor digitorum superficialis, flexor carpi ulnaris, flexor carpi radialis, and pronator teres.

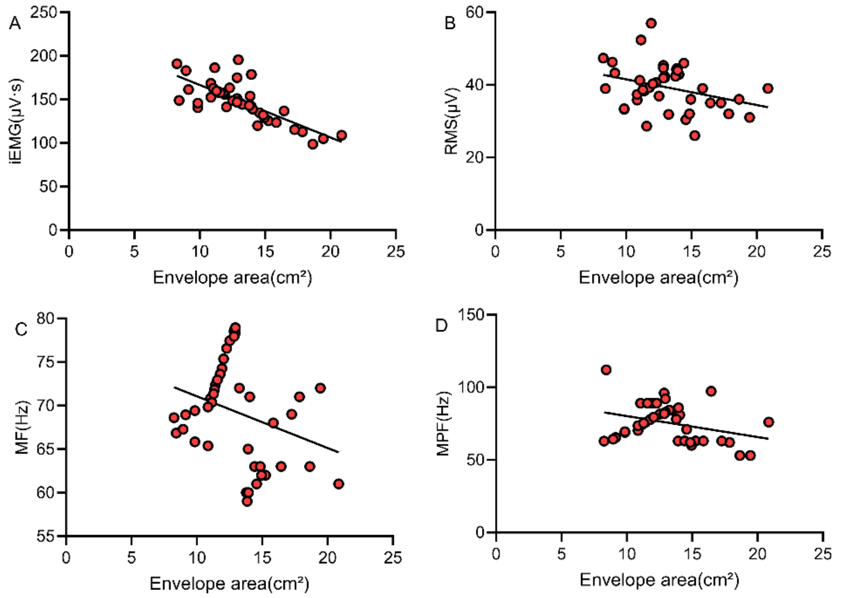

Figure 3 Correlation analysis between envelope area and EMG parameters

The envelope area was negatively correlated with iEMG (figure A), RMS (figure B), MF (figure C), and MPF (figure D) (P<0.05).

Table 4 Correlation analysis between sEMG signals and balance function parameters

	iEMG	RMS	MF	MPF
Trajectory length	r=-0.567	r=-0.107	r=-0.069	r=-0.109
	P<0.0001	P=0.035	P=0.046	P=0.032
Envelope area	r=-0.583	r=-0.107	r=-0.085	r=-0.108
	P<0.0001	P=0.034	P=0.049	P=0.033

3.6 Efficacy assessment based on MAS changes

Based on the MAS, 8 cases (19.05%) achieved complete recovery, 18 cases (42.86%) showed marked improvement, 14 cases (33.33%) demonstrated improvement, and 2 cases (4.76%) showed no response, with an overall effective rate of 95.24%.

3.7 ROC curve analysis of EMG parameters for evaluating upper limb spasticity recovery

ROC curves were plotted to evaluate the clinical value of the EMG parameters iEMG, RMS, MF, and MPF in assessing the clinical efficacy of enrolled patients. As only two patients showed no response in this study, making the evaluation challenging, the curves of EMG parameters for (complete recovery + marked improvement) and (improvement + no response) were plotted. The results showed that the AUCs for iEMG, RMS, MF, and MPF were 0.748, 0.731, 0.737, and 0.826, respectively ($P<0.05$) (**Figure 4**).

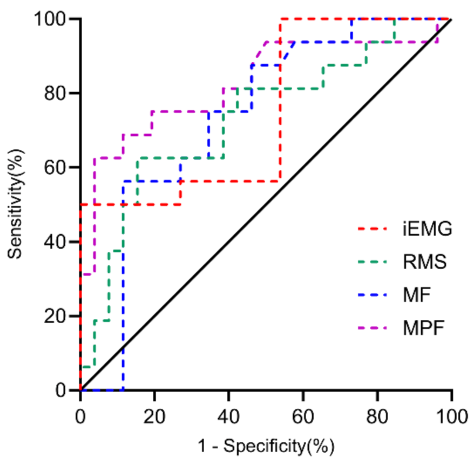

Figure 4 ROC curve analysis of EMG parameters for evaluating upper limb spasticity recovery

The AUCs for iEMG, RMS, MF, and MPF were 0.748, 0.731, 0.737, and 0.826, respectively ($P<0.05$).

4 Discussion

This study systematically evaluated 42 patients with post-stroke upper limb spasticity through combined multi-parameter sEMG analysis and MSS score. The results demonstrated that this integrated assessment method objectively and comprehensively reflects the functional status of the patients' upper limb, providing scientific evidence for clinical rehabilitation treatment. The findings are discussed in depth from multiple perspectives below.

4.1 Application value of sEMG parameters in spasticity assessment

This study found that at rest, the RMS and iEMG values of the affected forearm muscles were significantly higher than those of the unaffected side and the healthy control group. Among these muscles, the flexor pollicis longus showed the highest

RMS value, while the RMS values of all muscles in the healthy control group ranged from 5.7 to 12.5 μV. This finding is consistent with previous studies on abnormal electrical activity in spastic muscles at rest, which may reflect reduced regulation of inhibitory reflex pathways following upper motor neuron injury, leading to persistent non-autonomic electrical activity in muscles even during rest [12, 13]. Unlike previous studies that mainly focused on upper arm muscles, such as the biceps brachii and triceps brachii, this study simultaneously analyzed eight major forearm flexor and extensor muscles. The results showed that the degree of abnormal resting electrical activity differed among muscles, with flexor muscles (flexor pollicis longus and flexor digitorum superficialis) exhibiting greater abnormalities than extensor muscles. This finding is consistent with the typical flexor spasticity pattern observed after stroke [14, 15]. During active movement, the RMS values of all muscles on the affected side were significantly lower than those in the healthy control group, indicating marked impairment in motor unit recruitment during active contraction in the spastic limb. This phenomenon may be related to the decreased motor unit activation capacity caused by corticospinal tract dysfunction. Simultaneously, the persistent abnormal tension in spastic muscles may also affect maximal activation capacity during active contraction through an exhaustion mechanism [16]. In addition, the forearm muscles play a crucial role in the fine motor functions of the wrists and fingers. Their dysfunction directly affects patients' ability to perform activities of daily living, such as gripping and pinching. Therefore, precise assessment of forearm muscle function is of great clinical significance [17].

4.2 Correlation between sEMG and balance function and exploration of its mechanism

This study systematically analyzed the correlation between upper limb sEMG parameters and balance function, revealing that iEMG was negatively correlated with trajectory length and envelope area. This correlation reveals an intrinsic connection between upper limb function and overall postural control. From a neurophysiological perspective, this correlation may involve multiple mechanisms. First, the upper limbs play an important auxiliary role in maintaining balance. Research indicates that when the body balance is disturbed, the upper limbs generate a reaction torque by swinging to help maintain the stability of the center of gravity [18]. Post-stroke upper limb spasticity limits this compensatory mechanism, resulting in a decrease in balance control ability. Second, the overall recovery effect of the central nervous system should not be overlooked. The corticospinal tract innervates both the upper limb and trunk muscles, and its functional recovery concurrently improves upper limb motor control and postural stability [19]. Furthermore, improvements in sensorimotor integration are also crucial factors. Post-stroke proprioceptive impairments are common issues that affect the precision of motor control. Improvements in sEMG parameters reflect the restoration of sensory feedback loops, which are crucial for fine motor control and balance maintenance. This study examined the association between upper-limb sEMG parameters (rather than lower limb parameters) and balance function for several reasons. First, the primary objective was to evaluate upper-limb neuromuscular function. Exploring the association between upper-limb functional parameters and overall postural stability may facilitate a system-level understanding of neural functional reorganization after stroke. In addition, this approach provides a comprehensive functional reference for upper limb-oriented rehabilitation strategies, supporting integrated assessment. The association between lower-limb sEMG parameters and balance function has been extensively reported. This study aims to fill the gap in research related to the upper limbs. Further analysis of the results revealed that RMS, MF, and MPF showed only weak correlations with balance parameters, suggesting these parameters may primarily reflect localized muscle function. In contrast, iEMG, as a comprehensive indicator, better reflects the overall functional state of the neuromuscular system.

4.3 Advantages and clinical value of MSS score

In this study, patients demonstrated a significant improvement in their MSS total scores after intervention, which were markedly higher than those reported in traditional Fugl-Meyer assessments [19]. This discrepancy may be primarily attributed to the design characteristics of the MSS. The MSS uses a 6-point rating scale, which captures functional changes more accurately than the Fugl-Meyer's

3-point scale. This advantage is particularly evident during the subacute phase when patients experience rapid functional recovery, where the MSS demonstrates superior sensitivity. Analysis of various dimensions indicates that the enrolled patients demonstrated the most significant improvement in shoulder mobility after intervention. This may be attributed to the shoulder joint serving as the primary link in the upper limb kinetic chain, making it more likely to show improvement in the early stages of rehabilitation. Although the improvement in hand mobility was relatively small, its clinical significance remains considerable. The restoration of hand function directly impacts the ability to perform activities of daily living and is a core goal of rehabilitation therapy [20]. The MSS provides a detailed assessment of hand function, including fine motor skills such as thumb opposition, lateral pinching, and finger pinching, thereby providing a basis for developing targeted training programs.

4.4 Diagnostic value and clinical application of sEMG parameters

ROC curve analysis revealed that MPF exhibited the highest AUC value, indicating its optimal diagnostic value in predicting therapeutic efficacy. This finding has significant clinical implications. MPF reflects the center of gravity frequency of the power spectrum curve and is closely related to the conduction velocity of motor unit action potentials. A high MPF value indicates the preferential recruitment of fast motor units and good nerve conduction function, which is an important indicator of motor function recovery [21]. Based on the findings of this study, it is recommended to use MPF > 90 Hz as a reference threshold for predicting favorable rehabilitation outcomes. When patients exhibit high MPF values or a rapid upward trend in MPF during the early stages of treatment, better rehabilitation outcomes can be anticipated, enabling the formulation of more proactive rehabilitation strategies. Conversely, persistently low MPF values may indicate poor prognosis, necessitating adjustments to the treatment plan or increased intervention intensity. The AUC value of iEMG was 0.748, which was slightly lower than that of MPF, but still demonstrated good diagnostic value. As a comprehensive indicator reflecting overall muscle electrical activity, iEMG has the advantages of simplicity of detection and intuitive results in clinical applications. The diagnostic value of RMS and MF was relatively low, possibly because these parameters primarily reflect localized muscle characteristics and provide insufficient representation of overall functional status [22].

4.5 Clinical significance and translational applications

The comprehensive evaluation system established in this study has significant clinical translational value. First, this system achieves an organic integration of subjective and objective assessments. It retains the functional orientation of clinical scales while incorporating the objectivity of electrophysiological indicators, thereby improving the comprehensiveness and accuracy of the evaluation. Second, multi-parameter analysis provides a wealth of information dimensions, aiding in the identification of functional impairment characteristics of different patients and enabling precision rehabilitation. In addition, the standardized and quantitative characteristics of this assessment method provide a powerful tool for evidence-based evaluation of rehabilitation efficacy.

4.6 Research limitations and future prospects

This study has certain limitations that need to be considered when interpreting the results. First, the sample size was relatively small (n=42), and as a single-center study, it may be subject to selection bias. The generalizability of the findings requires validation through multicenter, large-sample studies. Second, the use of a self-controlled design without a parallel control group makes it difficult to completely rule out the influence of confounding factors such as natural recovery and placebo effects. Third, the study period was only 12 weeks, lacking long-term follow-up data, making it impossible to evaluate the sustainability of treatment effects and long-term prognosis. Fourth, other rehabilitation assessment indicators such as the modified Barthel index and quality of life scale were not included for comprehensive comparison, which may overlook some important functional dimensions. Future research should primarily focus on conducting multicenter, large-sample randomized controlled trials with extended follow-up periods of 6 months or 1 year to evaluate long-term efficacy. Additionally, efforts should be made to incorporate more assessment dimensions, such as activities of daily living, quality of life, and psychological status.

5 Conclusion

Multi-parameter sEMG analysis combined with MSS score enables objective and quantitative evaluation of functional status in post-stroke upper limb spasticity. Among these parameters, MPF and iEMG demonstrate high diagnostic value and serve as important indicators for predicting rehabilitation outcomes. This integrated evaluation method overcomes the subjective limitations of traditional assessment approaches, providing a scientific basis for formulating clinical rehabilitation treatment plans and evaluating their efficacy. Future studies should further validate its clinical value through large-sample, multicenter research and explore individualized rehabilitation strategies based on this assessment system.

Statements

Acknowledgement: None.

Statement of Ethics: The study protocol was approved by the ethics committee of Beijing Jishuitan Hospital, Capital Medical University.

Disclosure Statement: The authors have no conflicts of interest to declare.

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Author Contributions: Rao Wang and Wenjun Li conceived the project, designed and performed the experiments, analyzed the data and wrote the manuscript.

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