



Loading modulates monosynaptic transmission from spindle primary afferents to motoneurons in humans

Nilgün Yıldız¹ · Selim Sezikli² · Eser Kalaoglu² · İlhan Karacan^{2,3} · Kemal Sıtkı Türker⁴

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Abstract

The literature does not provide a consistent account of how mechanical loading influences H-reflex excitability. Given the methodological diversity across previous studies, the present study investigated how different levels of mechanical load affect soleus H-reflex excitability during quiet stance in healthy adults. It incorporated several experimental controls to enhance the reliability and comparability of results. Eighteen participants were tested under five load conditions (10–100% of body weight) while maintaining a consistent M-wave amplitude and a relaxed muscle posture. H-reflex amplitude decreased progressively with increasing load, reaching significant suppression at full weight-bearing ($F(4, 68) = 7.04$, $p < 0.001$, partial $\eta^2 = 0.293$), whereas background EMG activity showed an opposite trend ($\chi^2(4) = 26.97$, $p < 0.001$). This dissociation suggests that muscle spindle-based spinal reflex excitability does not scale linearly with muscle activation, indicating enhanced premotoneuronal modulatory control under higher loading. These findings highlight that spinal circuits dynamically adjust reflexes to stabilise posture, prevent excessive contractions and fine motor control in response to increasing mechanical demands.

Keywords Loading · H-reflex · Motoneurons · Muscle spindle · Human physiology · Synapse

Introduction

The Hoffmann (H-) reflex in humans is elicited by percutaneous electrical stimulation of a mixed peripheral nerve containing both sensory and motor fibres. This stimulation evokes two distinct electromyographic (EMG) responses in the corresponding (homonymous) muscle: the M-wave, representing the direct activation of motor axons, and the H-reflex, reflecting the monosynaptic excitation of α -motoneurons via Ia afferents (Palmieri et al. 2004).

The amplitude of the H-reflex provides an index of the net excitability of the monosynaptic reflex pathway, determined by both presynaptic and postsynaptic mechanisms. A range of physiological factors influences it. For example, an increase in background motoneuronal activity before stimulation linearly augments the H-reflex amplitude through an “automatic compensation” mechanism mediated by postsynaptic processes (Matthews 1986; Burke et al. 1989; Frigon et al. 2007).

Even when background activity is controlled, H-reflex amplitude varies systematically with body posture and movement. It is typically greatest in the prone or supine position, smaller in the sitting position, and lowest in the

✉ İlhan Karacan
ilhan.karacan@sbu.edu.tr

✉ Kemal Sıtkı Türker
ksturker@gelisim.edu.tr

Nilgün Yıldız
nilgyildiz@gelisim.edu.tr

Selim Sezikli
selim.sezikli@saglik.gov.tr

Eser Kalaoglu
eser.kalaoglu@saglik.gov.tr

¹ Department of Physiotherapy and Rehabilitation, Faculty of Health Sciences, Istanbul Gelisim University, Istanbul, Turkey

² İstanbul Physical Therapy Rehabilitation Training and Research Hospital, Istanbul, Turkey

³ Physical Medicine and Rehabilitation Department, Hamidiye Faculty of Medicine, Health Sciences University, Istanbul, Turkey

⁴ Physiology Department, Faculty of Dentistry, Istanbul Gelisim University, Istanbul, Turkey

standing position (Koceja et al. 1995; Cattagni et al. 2014; Qin et al. 2021; Cecen et al. 2018). A further reduction is observed when switching from bipedal to unipedal stance (Kim et al. 2013), and the reflex diminishes further during walking and running (Capaday and Stein 1986). These posture- and movement-related reductions have been attributed primarily to enhanced presynaptic inhibition of Ia afferent terminals projecting onto the motoneuron pool (Cecen et al. 2018).

Studies examining modulation of the soleus H-reflex amplitude under different standing loading conditions have yielded conflicting results. Hwang et al. (2004) reported that the soleus H/M ratio did not differ significantly across 10%, 50%, and 90% bodyweight bearing in healthy adults. Similarly, Phadke et al. (2006) found no significant effect of loading on the H-reflex response, and Ali and Sabbahi (2000) observed no difference between loading and unloading conditions. In contrast, Hwang et al. (2011) showed that as body weight increased, the soleus H-reflex amplitude increased, and the H/M ratio was positively correlated with load. Conversely, when background EMG activity was controlled, Miyoshi et al. (2003) showed that increased loading did not enhance but somewhat suppressed reflex excitability.

Taken together, the literature does not provide a consistent account of how loading influences H-reflex excitability. In view of the methodological diversity among previous studies (summarised in Table 1), the present investigation incorporated several experimental controls designed to enhance the reliability and comparability of results.

The study incorporated the following control procedures:

1. The background surface EMG level preceding each stimulus was recorded.
2. Stimulus intensity was adjusted as required to maintain a constant M-wave amplitude across all loading conditions.
3. All measurements were obtained during natural standing on the right heel.
4. H-reflex amplitudes were assessed at five loading levels: 10%, 30%, 50%, 70%, and 100% body weight.

This study, therefore, aimed to characterise how the soleus H-reflex is modulated by progressively increasing mechanical loads and to assess how background muscle activity (BGA) changes in response to these loads, as variations in posture and muscle activation may have contributed to inconsistencies in previous findings. Given that load-related changes reported in earlier studies may have reflected uncontrolled fluctuations in voluntary activation, postural adjustments, or M-wave instability rather than the isolated effect of mechanical load, the present investigation sought to determine how both H-reflex amplitude and background EMG vary with increasing load magnitude.

Methods

Participants

A total of 22 participants were initially recruited for the study. All participants were between 18 and 45 years of

Table 1 Summary of studies on the effect of loading on H-reflex

Studies	Loading conditions	Stance	Background EMG Analysis	Stimulus condition	Effect on H-reflex size
Ali and Sabbahi (2000)	Prone lying, standing, lifting + 20% BW, unloading - 25% BW	Bipedal	-	M-wave not controlled	↓ Standing, loading, unloading < prone; no difference among standing/loading/unloading
Miyoshi et al. (2003)	NG, HG, MG	Bipedal	+	M-wave constant (10 ± 5% Mmax)	↑ in both HG and MG vs. NG (lowest in NG; HG increase linked to BGA, MG increase linked to reduced presynaptic inhibition)
Hwang et al. (2004)	Sitting, 10%, 50%, 90% body weight (BW) using external suspension systems	Sitting, unipedal	-	M-wave constant (10 ± 3% Mmax)	No difference among 10–90% BW loads; ↓ in standing vs. sitting
Phadke et al. (2006)	100% and 60% BW using external suspension systems	Bipedal	-	M-wave constant (10 ± 3% Mmax; intensity readjusted as needed)	No significant difference between 60% and 100% BW
Hwang et al. (2011)	100%, 90%, 80%, 70%, 60%, and 50% BW	Bipedal	+	M-wave constant (3–7% of Mmax)	↑ H-reflex amplitude increased with higher BW load (100%, 90% > 70–50% BW)
Kim et al. (2013)	Prone, bipedal, unipedal	Bipedal, unipedal	+	NA	↓ Reduced in unipedal stance (for both FL and SOL)
Current study	10, 30, 50, 70 and 100% BW	Unipedal	+	M-wave constant (10–30% Mmax)	

BW=body weight; NG=normal gravity; HG=hypergravity; MG=microgravity; FL=fibularis longus; SOL=soleus; NA=Not Available; - indicates that those authors have not reported background activity levels preceding the H-reflex; + Did

age and had no history of musculoskeletal, neurological, or orthopaedic disorders. Four participants were excluded because an H-reflex could not be elicited, a maximal M-wave (Mmax) could not be obtained, or the experimental protocol could not be completed. Consequently, the study was completed with 18 healthy adults (11 males and 7 females; mean age 27.4 ± 5.4 years), and all statistical analyses were performed using data obtained from these 18 participants. All participants received a detailed explanation of the study procedures before testing and provided written informed consent in accordance with the Declaration of Helsinki. The experimental protocol was approved by the local ethics committee (Koc University Human Ethics Committee Approval No: 171 2017.124.IRB2.038).

Stimulation protocol

The soleus H-reflex was assessed under five different loading conditions applied to the right heel:

1. 10% of body weight (BW).
2. 30% BW.
3. 50% BW.
4. 70% BW.
5. 100% BW.

Initially, the soleus tendon reflex (T-reflex) was recorded using an electronic reflex hammer (MLA93, AD Instruments, UK) to verify reflex responsiveness. To elicit the H-reflex, a 1 cm diameter hemispherical cathode electrode was positioned over the tibial nerve in the right popliteal fossa, and a 10×12 cm rectangular anode electrode was placed over the suprapatellar region. Both electrodes were secured with an elastic bandage. Monophasic square-wave stimuli of 1 ms duration were delivered using a constant-current stimulator (DS7A, Digitimer, Hertfordshire, UK).

The H-reflex was then tested while participants stood quietly in an anatomical neutral posture, lightly holding onto a fixed bar at elbow height for balance, with their feet approximately shoulder-width apart, corresponding to $\sim 50\%$ BW on the right heel. At this position, the Mmax was obtained by incrementally increasing stimulus intensity until a plateau in the M-wave was observed.

The stimulation intensity required to evoke an M-wave corresponding to 10–30% of Mmax, which induced H-reflex in the rising phase of the H/M curve, was determined. Using this intensity, H-reflex responses were recorded under the five loading conditions, presented in randomised order to minimise sequence effects.

In each of the five experimental conditions, ten stimuli were delivered at this predetermined intensity. The constancy of the M-wave amplitude was continuously verified

to ensure stimulus stability. The stimulus intensity was adjusted as needed to achieve the predetermined M-wave amplitude for each stimulus. When the M-wave amplitude was different from the set value, the stimulus intensity was adjusted as necessary and the number of stimuli was increased to obtain at least 10 good records. The tibial nerve was stimulated with a minimum interstimulus interval of 10 s to prevent post-activation depression. The stimuli were randomly separated by 10–14 s to prevent prediction.

Surface electromyography recording

sEMG recordings were obtained from the right soleus muscle using self-adhesive bipolar Ag/AgCl electrodes (Redline[®], Istanbul, Türkiye; 10 mm diameter; 4 cm inter-electrode distance, aligned parallel to the muscle fibres) after standard skin preparation to reduce impedance below 10 k Ω . The electrodes were placed over the lateral belly of the soleus muscle, and the ground electrode was positioned on the right lateral malleolus. Signals were amplified $\times 1000$, band-pass filtered (10–1,000 Hz), and sampled at 5,000 Hz (Tucker and Türker 2005). All signals were visually monitored in real time and stored for offline analysis. During all measurements, participants were instructed to maintain a relaxed posture and to avoid voluntary contraction of the calf muscles. Background EMG activity was continuously monitored.

Recording loading data

Participants placed their right heel comfortably on a force plate (FC2231-0000-0100-L Compression Load Sensor, France) embedded in the whole body vibration (WBV) platform. They were instructed to shift their body weight onto the test leg without flexing the hip or knee joints. A real-time visual display of vertical ground reaction force (GRF) on a monitor allowed participants to maintain the required load distribution throughout each trial. The force signals were amplified 100-fold, filtered between DC and 300 Hz, and sampled at 5000 Hz.

Data acquisition and analysis

sEMG and force signals were acquired using *Spike2* software (version 7.20; Cambridge Electronic Design, Cambridge, UK), interfaced with a CED 1902 Quad System MK III amplifier and a CED Power 1401 MK II analogue-to-digital converter (model 3601). Data were analysed offline using *Spike2* software.

A 30 Hz high-pass filter was applied to the EMG signals before analysis to minimise movement artefacts (Karacan et al. 2023; Karacan and Türker 2025). The peak-to-peak

amplitude of Mmax was measured, and for each condition, the average of ten H-reflex responses was computed. The H-reflex peak-to-peak amplitudes were then normalised to Mmax to account for interindividual variability and expressed as H/Mmax.

To quantify background EMG activity, raw EMG signals were full-wave rectified and averaged across trials for each condition. Background activity (BGA) was defined as the mean rectified EMG amplitude during the 1-s interval preceding the stimulus onset. For each participant, these values were normalised to the maximum EMG activity during an attempted maximal contraction, with the person plantarflexing maximally in the tiptoe position.

Statistical analysis

Data are expressed as the arithmetic mean $\pm$ standard deviation (SD) and were analysed using SPSS v29 (SPSS Inc., Chicago, IL, USA). Normality was assessed with the Shapiro–Wilk test. H/Mmax ratios were compared by repeated-measures ANOVA (partial η^2 as effect size). BGA were compared using the Friedman test with Bonferroni-adjusted post hoc comparisons, and effect sizes (r) were reported. For the Bonferroni correction, the alpha level was divided by the number of pairwise comparisons (10) among the five loading conditions.

To address the association between background EMG activity and H-reflex modulation at the participant level, a linear mixed model was additionally performed with H/

Mmax as the dependent variable, loading condition as a fixed factor, BGA as a covariate, and participant as a random effect. This analysis was used to determine whether BGA was independently associated with H/Mmax after accounting for the repeated-measures structure of the data and the common effect of loading condition.

A post hoc power analysis based on the observed effect size ($\eta^2_p = 0.293$), sample size ($n=18$), and $\alpha=0.05$ indicated a statistical power of 1.00. The effect size r indicates both the strength and the direction of the effect and can be positive or negative. A negative r means that the second condition has a lower value than the first. Values around 0.10 indicate a small effect, around 0.30 a medium effect, and 0.50 or higher a significant effect. In contrast, partial eta squared (partial η^2) reflects the proportion of variance explained by the factor, is always positive, and is interpreted as small (≈ 0.01), medium (≈ 0.06), or large (≥ 0.14) (Cohen 1988).

Results

H/Mmax ratios were found to differ significantly when compared in five different positions ($F_{(4, 68)}=7.04$, $p<0.001$, partial $\eta^2 = 0.293$). The H-reflex response was suppressed more at 100% loading than at the other four loadings. Figure 1 illustrates the mean normalised H-reflex amplitudes and BGA across five different loading conditions (10–100%). As the load increased, H-reflex amplitude tended to decrease, whereas BGA amplitude increased progressively.

Post-hoc pairwise comparisons, including Bonferroni-adjusted p values and effect sizes, are presented in Table 2. For H/Mmax, significant differences were observed between 100% loading and 10%, 30%, 50%, and 70% loading, indicating greater H-reflex suppression at the highest loading level. When the BGA was examined, significant differences were observed between 10% and 50%, 70%, and 100% loading, as well as between 30% and 100% loading, with activity increasing with loading.

To examine the participant-level association between background EMG activity and H-reflex amplitude, an initial Spearman correlation analysis was performed using all individual participant data across loading conditions. This analysis demonstrated a weak negative association between BGA and H/Mmax (Spearman's $\rho = -0.218$, $p=0.040$) (Fig. 2). However, to determine whether this association persisted after accounting for the common effect of mechanical loading, a linear mixed model was performed with H/Mmax as the dependent variable, loading condition as a fixed factor, BGA as a covariate, and participant as a random effect. The analysis demonstrated a significant main effect of loading condition on H/Mmax ($F_{(4,66.993)}=5.414$, $p=0.001$),

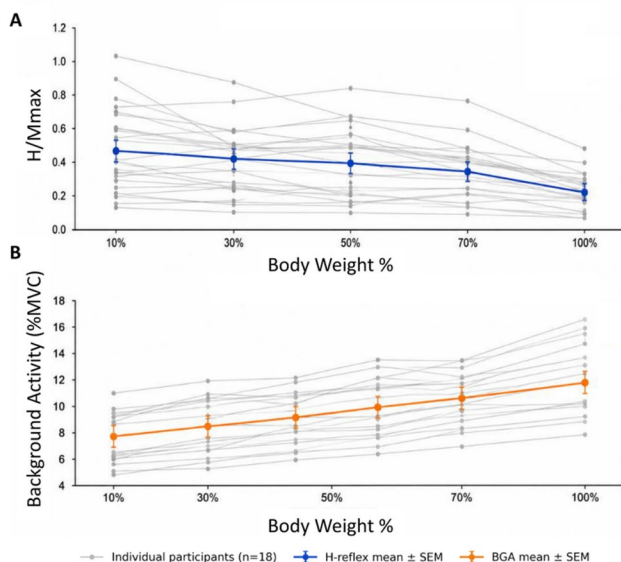


Fig. 1 Changes in normalised H-reflex amplitude (H/Mmax) and background EMG activity (%MVC) across five loading conditions (10–100% body weight). Grey lines represent individual participant responses, while colored lines represent group mean $\pm$ SEM values for H-reflex amplitude (blue) and BGA (orange). Overall, H-reflex amplitude decreased, whereas BGA increased with increasing load

Table 2 Pairwise comparisons of background EMG activity and H/Mmax across different loading levels

Comparison	Background sEMG activity		H/Mmax	
	<i>p</i> (adjusted)	Effect size (<i>r</i>)	<i>p</i> (adjusted)	Effect size (<i>d</i>)
10% vs. 30%	1.000	−0.499	1.000	−0.087
10% vs. 50%	0.034	−0.718	1.000	0.113
10% vs. 70%	0.002	−0.764	1.000	0.155
10% vs. 100%	0.000	−0.844	0.012	0.930
30% vs. 50%	0.509	−0.559	1.000	0.162
30% vs. 70%	0.067	−0.601	1.000	0.195
30% vs. 100%	0.008	−0.662	0.005	1.008
50% vs. 70%	1.000	−0.334	1.000	0.039
50% vs. 100%	1.000	−0.436	0.004	1.002
70% vs. 100%	1.000	−0.344	0.008	0.933

The table summarises the results of post hoc pairwise comparisons between loading conditions. For each comparison, Bonferroni-adjusted *p*-values and effect size estimates (*r* for background EMG; Cohen's *d* for H/Mmax) are provided to indicate the magnitude of differences across loading conditions

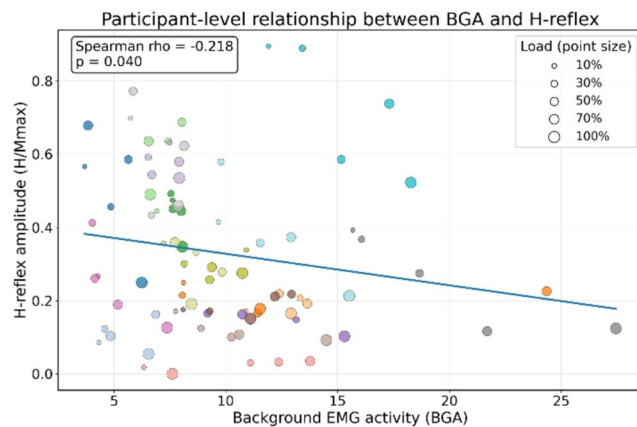


Fig. 2 Participant-level relationship between background EMG activity (%MVC) and normalised H-reflex amplitude across loading conditions. Each colored point represents an individual observation, with color indicating the participant and the size of the points indicating the loading condition. Larger points correspond to higher loading levels. The blue line represents the overall linear trend across all observations

indicating that H-reflex amplitude was significantly modulated by increasing mechanical load. In contrast, BGA was not independently associated with H/Mmax after accounting for loading condition ($F(1,77.781)=3.283, p=0.074$).

Discussion

The main finding of this study was that the soleus H-reflex amplitude decreased progressively with increasing load, with significant suppression at full weight-bearing in the unipedal condition (100% BW). Conversely, BGA of the soleus muscle increased in parallel with load. This

dissociation—reflex suppression despite elevated muscle activation—suggests modulation at the premotoneuronal level rather than changes in postsynaptic excitability. Presynaptic inhibition, recurrent inhibition and reciprocal inhibition are plausible premotoneuronal mechanisms. Increased afferent inflow during loading likely contributes to postural stability by reducing the H-reflex.

The literature presents mixed findings on the effects of loading on the H-reflex (Table 1). Some studies (Phadke et al. 2006; Ali and Sabbahi 2000) found no significant effect of loading, but these were conducted in symmetrical bipedal stance and employed an external suspension system, which reduces postural and sensory demands. Hwang et al. (2004) also found no change despite manipulating load by shifting body weight onto the tested limb, but their protocol reached only 90% unilateral loading. Later, the same group, Hwang et al. (2011), employed a bilateral stance without any suspension system and observed an increase in H-reflex amplitude as overall vertical loading increased. Importantly, however, the “loading levels” reported in that study (50–100% BW) were not experimentally imposed but instead reflected natural variations in bilateral weight distribution measured with dual force platforms. Thus, the apparent load-related facilitation of the H-reflex most likely reflects increased background muscle activation associated with subtle postural shifts rather than the neurophysiological effects of accurate mechanical loading, as force development can be influenced by activation of various afferent feedback pathways (Lecce et al. 2026).

A more mechanistically revealing perspective emerges from Miyoshi et al. (2003), who experimentally dissociated gravitational loading from voluntary muscle activation using a parabolic-flight model. Their findings demonstrate that H-reflex amplitude can vary independently of BGA when the load-sensitive somatosensory channels that regulate Ia-terminal presynaptic inhibition are selectively manipulated. Specifically, under microgravity, the background EMG of the soleus was nearly abolished, yet the H-reflex amplitude became *larger* than in normal gravity. Conversely, during hypergravity, both BGA and H-reflex increased. Still, covariance analysis revealed that the reflex facilitation was entirely attributable to the rise in BGA and not to gravitational load per se. The critical insight is that the H-reflex gain during natural stance is typically suppressed by load-related afferent inputs, which increase presynaptic inhibition at Ia terminals. Removal of these afferent signals in microgravity effectively *releases* the presynaptic inhibition, resulting in a disproportionate increase in H-reflex amplitude despite minimal muscle activation. Thus, Miyoshi’s study underscores that actual mechanical load exerts a net inhibitory effect on the spinal stretch reflex pathway, mediated predominantly through presynaptic mechanisms rather

than changes in postsynaptic excitability or background activation.

In this context, our finding that H-reflex amplitude progressively decreased with increasing unilateral load aligns more closely with the mechanistic interpretation provided by Miyoshi et al. (2003) than with studies reporting load-related facilitation. The discrepancy with the latter literature likely reflects differences in postural constraints, muscle activation strategies, and the extent to which experimentally imposed load isolates the mechanosensory sources that govern Ia-terminal presynaptic inhibition. Together, these observations reinforce the need to control both M-wave stability and background activation when assessing load-dependent spinal excitability and highlight the dominant role of load-encoding somatosensory pathways in shaping H-reflex behaviour during upright stance.

Similarly, Kim et al. (2013) demonstrated that H-reflex amplitude in the soleus and fibularis longus varied with body position and was significantly suppressed during single-leg stance. This observation parallels our finding that reflex gain decreases under unilateral loading, supporting the notion that spinal reflex modulation intensifies as postural control demands increase. Thus, the H-reflex appears to be influenced not only by the magnitude of the mechanical load but also by the distribution of the load (unilateral vs. bilateral), the associated postural stability requirements, and the interaction among converging afferent inputs.

Interaction between voluntary drive and reflex modulation

Based on isolated muscle contractions, the H-reflex amplitude typically increases with greater pre-stimulus BGA. Contrary to expectations, we found that loading-induced increases in BGA were accompanied by a reduction in the H-reflex amplitude. This inverse linear relationship suggests that loading exerts potent presynaptic/premotoneuronal inhibition on the synaptic effectiveness of spindle primary afferents projecting to homonymous motoneurons. Along this line, it has been recently shown that the spindle feedback can be flexible when task demands change (Olson et al. 2025a, b).

During voluntary contraction, excitatory descending inputs from corticospinal and brainstem pathways depolarise α -motoneurons, facilitating reflex transmission (Zehr 2002). Accordingly, H-reflex amplitude typically scales with voluntary BGA (Burke 1983; Zehr 2002; Knikou 2008; Frigon et al. 2007). Several studies (e.g., Batista-Ferreira et al. 2022; Pensini and Martin 2004) confirmed that modest increases in EMG during low-to-moderate contractions enhance H-reflex amplitude, reflecting synergistic integration of voluntary and reflex pathways.

In the present study, BGA increased progressively with increasing mechanical load, whereas H-reflex amplitude decreased, particularly under the highest loading condition. This indicates that H-reflex amplitude did not simply increase in parallel with background muscle activity under high-load conditions. However, the participant-level mixed model showed that BGA was not independently associated with H/Mmax after accounting for the loading condition. Thus, the reduction in H-reflex amplitude is more appropriately interpreted as a load-dependent modulation of reflex excitability rather than as evidence of a direct association between BGA and H-reflex suppression.

Several mechanisms may contribute to load-dependent modulation of the H-reflex, including presynaptic inhibition of Ia afferents, premotoneuronal influences, recurrent inhibition, reciprocal inhibition, and supraspinal modulation (Morita et al. 2001; Nielsen et al. 1993; Pierrot-Deseilligny and Burke 2005). Nevertheless, these mechanisms were not directly measured in the present study and therefore cannot be confirmed from the current data. These interpretations should be regarded as hypothesis-generating and require confirmation in future studies using experimental approaches that directly assess spinal inhibitory and supraspinal mechanisms.

Receptor origin

The premotoneuronal inhibition of Ia terminals observed under higher mechanical loads is likely mediated by slowly adapting mechanoreceptors that encode sustained increases in weight-bearing. Candidate inputs include cutaneous and subcutaneous pressure receptors on the heel, particularly Ruffini and Merkel endings, which provide tonic load-related afferent feedback (Kennedy and Inglis 2002; Strzalkowski et al. 2018). However, because the heel skin contains predominantly rapidly adapting mechanoreceptors that are less sensitive to static pressure (Strzalkowski et al. 2015; Purves et al., 2001), applying the load through the heel was intended to minimise cutaneous input during the task, thereby allowing load-dependent spinal modulation to be examined with reduced confounding from skin afferents. There is also a suggestion that osteocytes—whose mechanoelectrical transduction is driven by strain-induced fluid shear within the lacuno-canalicular network—may contribute to load-dependent modulation of spinal excitability by providing a continuous afferent bias onto interneuronal circuits governing Ia presynaptic inhibition (Karacan et al. 2017; Sezikli et al. 2026). Notably, the profound reduction of skeletal strain in microgravity markedly attenuates osteocyte-mediated mechanosensory signalling (Karacan and Türker 2026). This mechanism aligns closely with the findings of Miyoshi et al. (2003), who demonstrated that

removing load in microgravity releases Ia terminals from presynaptic inhibition and, consequently, produces a disproportionate increase in H-reflex amplitude despite minimal background activation. Taken together, activation of these mechanosensitive pathways may contribute to the load-dependent increases in background muscle activity observed in the present study (Karacan and Türker 2026).

Clinical relevance

These mechanisms can be considered protective modulators that preserve motor output stability and movement precision by preventing excessive amplification of reflex responses, even when motor drive is elevated. Our findings indicate that, under high loading conditions, reflex pathways operate at a distinct level of control, and the H-reflex does not respond linearly to increased motoneuronal activity.

Methodological considerations

In this study, participants were instructed to stand on their right heel to minimise mechanoreceptor activation in the metatarsal region during loading. Slowly adapting cutaneous receptors in the metatarsal region, such as Merkel discs, are known to be tonically active during quiet standing (Trulsson 2001), and their activation reduces the amplitude of both the soleus H-reflex and the stretch reflex (Knikou 2007; Sayenko et al. 2009). Because the heel skin contains predominantly rapidly adapting mechanoreceptors that are less sensitive to static pressure (Strzalkowski et al. 2015; Purves et al., 2001), applying the load through the heel was intended to minimise cutaneous input during the task, hereby reducing confounding sensory influences on load-related modulation of the H-reflex.

Participants also lightly touched a fixed bar at elbow height to maintain balance. Light touch reduces postural sway via haptic feedback without providing meaningful mechanical support (Jeka 1997; Lackner et al. 1999). Consequently, the postural challenge associated with unilateral loading—and the related supraspinal contributions, including vestibular influences—was likely attenuated (Goulart et al. 2000).

Strengths and limitations of the study

This study provides a rigorous, controlled characterisation of load-dependent modulation of the Ia- α motoneuron pathway. The combination of graded unilateral loading, precise M-wave stabilisation, and quantified background EMG enabled an isolated assessment of how mechanical load alters spinal excitability. Performing all measurements in unipedal stance, a posture that maximises postural and

afferent demand, further revealed a precise dose–response suppression of the H-reflex under increasing load. Together, these methodological features address key limitations of earlier studies and offer physiologically robust evidence for load-induced modulation of spinal circuitry.

Nevertheless, several limitations should be considered. Presynaptic inhibition was not directly assessed, and therefore, the specific inhibitory pathways underlying the observed suppression cannot be conclusively identified. Additionally, although heel loading effectively minimised but did not completely eliminate metatarsal cutaneous input, it may have introduced biomechanical biases and allowed residual activation of slowly adapting mechanoreceptors under sustained pressure. These factors may have contributed modestly to the observed reflex modulation and may limit generalisability to dynamic or full-foot-loading tasks.

Conclusion

Increasing load led to higher soleus EMG activity, reflecting greater motor unit recruitment, while simultaneously reducing H-reflex amplitude, indicative of augmented monosynaptic, spindle-mediated reflex inhibition. These results show that spindle-mediated reflex excitability does not scale linearly with muscle activation and that inhibitory mechanisms are progressively recruited under higher loading to maintain postural stability and fine motor control. These findings support the notion that load-dependent modulation of spinal excitability serves as a fine-tuning mechanism for neuromuscular stability during weight-bearing tasks. Future studies should directly assess the inhibitory circuits underlying load-dependent reflex suppression and determine whether these mechanisms generalise to dynamic tasks and clinical populations.

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Author contributions N.Y. performed the experiments, prepared the figures, analysed the results; S.S. performed the experiments, prepared the figures, analysed the results; E.K. performed the experiments, prepared the figures, analysed the results; I.K. conceived the project, performed the experiments, prepared the figures, analysed the results; wrote the paper; supervised the project; K.S.T. conceived the project, performed the experiments, prepared the figures, analysed the results; wrote the paper; supervised the project. All authors reviewed the manuscript and agreed on the submitted version.

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Declarations

Competing interests The authors declare no competing interests.

Ethical approval Authors confirm that they have read the Journal's position on issues involved in ethical publication and affirm that this report is consistent with those guidelines.

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