

Virtual reality does not fool the brain only: spinal excitability changes during virtually simulated falling

Sidney Grosprêtre, Pauline Eon, Philémon Marcel-Millet

▶ To cite this version:

Sidney Grosprêtre, Pauline Eon, Philémon Marcel-Millet. Virtual reality does not fool the brain only: spinal excitability changes during virtually simulated falling. Journal of Neurophysiology, 2023, 129, pp.368 - 379. 10.1152/jn.00383.2022 . hal-04500807

HAL Id: hal-04500807 https://hal.science/hal-04500807

Submitted on 12 Mar 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



RESEARCH ARTICLE

Control of Movement

Virtual reality does not fool the brain only: spinal excitability changes during virtually simulated falling

🕫 Sidney Grosprêtre, 🖻 Pauline Eon, and Philémon Marcel-Millet

Laboratory Culture Sport Health and Society (C3S-UR 4660), Sport and Performance Department, University of Franche-Comté, Besançon, France

Abstract

Virtual reality (VR) is known to induce substantial activation of brain's motor regions. It remains unclear to what extent virtual reality can trigger the sensorimotor system, and more particularly, whether it can affect lower nervous levels. In this study, we aimed to assess whether VR simulation of challenging and stressful postural situations (Richie's plank experience) could interfere with spinal excitability of postural muscles in 15 healthy young participants. The H-reflex of the triceps surae muscles was elicited with electrical nerve stimulation while participants were standing and wearing a VR headset. Participants went through several conditions, during which stimulations were evoked: standing still (noVR), standing in VR on the ground (groundVR), standing on the edge of a building (plankVR), and falling from the building (fallingVR). Myoelectrical activity of the triceps surae muscles was measured throughout the experiment. Leg and head movements were also measured by means of accelerometers to account for body oscillations. First, no differences in head rotations and myoelectrical activity were to be noted between conditions. Second, triceps H-reflex (H_{MAX}/M_{MAX}) was not affected from noVR to groundVR and plankVR. The most significant finding was a drastic decrease in H-reflex during falling ($-47 \pm 26.9\%$ between noVR and fallingVR, P = 0.015). It is suggested that experiencing a postural threat in VR efficiently modulates spinal excitability, despite remaining in a quiet standing posture. This study suggests that simulated falling mimics the neural adjustments observed during actual postural challenge tasks.

NEW & NOTEWORTHY The present study showed a modulation of spinal excitability induced by virtual reality (VR). In the standing position, soleus H-reflex was downmodulated during a simulated falling, in the absence of apparent changes in body oscillations. Since the same behavior is usually observed during real falling, it was suggested that the visual cues provided by VR were sufficiently strong to lead the neuromuscular system to mimic the actual modulation.

drop jump; H-reflex; Richie's plank; soleus; virtual reality

INTRODUCTION

Virtual reality (VR) is a digital simulation of a threedimensional environment, displayed to an individual who can interact with it. The display is often performed through a headset equipped with one screen in front of each eye. The advantage of this equipment lies in its particularly efficient simulation of a real context, to the point where the participant can be totally immersed. VR is now a tool widely used in many fields, from the industry, with driving simulators (1), to physical rehabilitation (2). For instance, the literature on VR-based interventions shows significant benefits on executive functions in patients with chronic stroke (3). The effect of VR is associated with the large neural activation it stimulates, particularly in the brain's motor regions. Studies using neuroimaging have shown that VR of seemingly real environments activates the supplementary motor areas, primary motor cortex, and cerebellum (4–8). Many authors argue that the mirror neuron system, first described by Gentilucci et al. (9) in the late 1980s, plays a major role in this valuable effect of VR on executive and motor functions (4, 8, 10). Indeed, VR induces considerable brain activation at the level of the sensorimotor regions, which could correspond to the mirror system, particularly when participants can interact within their virtual environment (11).

Submitted 12 September 2022 / Revised 18 November 2022 / Accepted 13 December 2022

Downloaded from journals.physiology.org/journal/jn (037.174.106.051) on March 12, 2024.

Correspondence: S. Grosprêtre (sidney.grospretre@univ-fcomte.fr).

The immersion effect is greater in case of simultaneous stimulation of several sensory systems, compatible with the simulated situation (12). The ability to freely navigate the virtual environment and interact with virtual objects contributes greatly to the sense of realism (13, 14). In the fields of rehabilitation and training, VR is widely used during gait and walking (15, 16). For instance, VR is an effective tool to modulate postural control in patients with stroke, when it is applied during standing (17). In addition, previous studies showed that static virtual environments did not challenge postural control (18–20), contrary to dynamic simulated situations (19, 21). Therefore, combining sensorimotor information from an actual standing posture with VR simulation appears to be an ideal approach to maximize the effects of such an intervention, especially on visual-motor abilities and on the neural system in general (22).

Spinal networks are also widely involved in controlling balance, especially those mediating the Ia afferent -to α motoneurons pathway such as presynaptic inhibitory circuits (23). Lower limb spinal excitability, usually assessed by recording the H-reflex through electrical stimulation of a mixed nerve, has been shown to be modulated downward as the complexity of the postural tasks increases (23-26). To date, this modulation has not been associated with leg muscle activity, but rather with body position (24). In a more unstable and challenging position, such as on a beam raised above the floor, the H-reflex is even more reduced compared with a quiet standing position (27). As the spinal excitability decreases along with an increase of the cortical somatosensory evoked potential, a shift toward more supraspinal motor control was suggested to occur during challenging postural tasks (28). The downward modulation of the H-reflex in such conditions was also suggested to be linked to the level of anxiety generated by the fear of falling (29). However, in quiet standing, a modulation of H-reflex is not always observed according to the level of postural threat, for instance when participants are physically placed at different heights up to 3 m (30). The postural threat is, however, known to induce changes in postural, autonomic, and psycho-social responses, whether the threat is real or virtually simulated (31).

Therefore, it remains unclear to what extent virtually simulated postural challenging tasks can trigger the neuromuscular system, especially the spinal reflex pathway. Several clues in the literature show that real and virtual postural tasks share similar effects on gait and autonomic responses (31), raising that the motor system and more particularly the spinal excitability can also potentially respond similarly. However, the literature often uses virtual situations that are physically acceptable, e.g., not more than jumpable heights, because the aim is to compare to real situation. The interest of virtual reality is also that it allows to push this limit to extreme situations that are not reproducible in real conditions, such as falling from very important heights (i.e., from the top of a building). The aim of this study was therefore to assess whether VR simulation of postural tasks, comprising a wide range of postural threat from standing quietly to free falling, could interfere with the spinal excitability of postural muscles. We hypothesized that a virtually simulated postural threat would be a sufficiently strong visual stimulus to induce the same downward modulation of the H-reflex pathway as observed in actual complex postural tasks. More particularly, free falling simulated through VR would lead to greater relative changes of the reflex pathway as compared with less threatening situations (standing at ground level).

METHODS

Participants

Fifteen healthy young participants (age: 27.2 ± 4.9 yr old; height: 172.9 ± 8.3; weight: 70.3 ± 15.7 kg; 5 women) provided written informed consent to participate in the present experiment. Our sample size calculation is based on the primary efficacy outcome that relates to changes in H-reflex amplitude with various interventions, such as motor imagery (32). The power calculation was performed with the software G*power (Kiel, Germany), considering a significance level of 5%, a power of 90%. Twelve participants were needed to meet the objectives of the study. All participants agreed not to participate in any unusual physical or cognitive activity before the protocol and to avoid intense exercise before the tests. All participants were free of any neurological or musculoskeletal disorders. The study protocol was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki. None of the participants had prior experience of VR practice.

VR Setup

For the VR experiments, we used Occulus Quest V2 headsets (Meta Platforms, Irvine, CA), which display images at $1,832 \times 1,920$ pixels and at a refresh rate of 120 Hz. The headset is linked to two wireless handles used to control the interface. The system is a 6 degrees of freedom (DoF) VR. In addition to having a 360° view (3 DoF), 6-DoF systems also enable participants to move around freely in their environment beyond their peri-personal space. They were free to move around the space thanks to wireless electrodes fixed to their leg for the purposes of the experiment. In the present experiment, the boundaries for the virtual space were set at 4 m long and 2 m wide (8 m^2) so that participants could fully experience the VR environment. The application used the game called Richie's Plank Experience (Toast company, Brisbane, Australia), which consists in displaying a computer-generated virtual three-dimensional urban environment. The game recreates a skyscraper landscape, where participants can walk on the street. Then, they take an elevator to the top of a building, which opens directly onto a plank suspended in mid-air at a height of 80 floors above the ground. They can walk onto the plank and even fall from it. Here, the plank was set to be 2 m long and 40 cm wide, to enable participants to take a few steps on it and stand naturally. Another option in the application offers the opportunity to pilot reactors placed in the player's hands, which allow the player to fly off the building and control the aerial displacement. In standing quiet posture, with or without VR, participants were asked to focus on a point at 2 m distance, which corresponds to the end of the plank. This was done to minimize the effect of gaze distance in-between VR and non-VR conditions.

Study Design

After a familiarization session to assess participants' tolerance for VR and to ensure that no motion sickness occurred, participants had one visit to the laboratory. The tests were carried out in one experimental session of about 1 h 30 min. After skin preparation and electrode positioning, the optimal stimulation site and intensities for triceps surae H-reflex and M-wave measurement were determined. These assessments were performed in a quiet standing position. Once the optimal stimulation parameters were identified, participants underwent five experimental conditions, in random order (Fig. 1).

Standing still (noVR).

Participants were asked to stand with their arms relaxed. They did not wear the VR headset in this condition.

Standing in VR on the ground (groundVR).

Participants stood on a calm street in the VR environment. After a few steps in the new environment, they were asked to stand quietly on the sidewalk with their arms relaxed.

Standing on a plank (plankVR).

After taking the elevator, participants were asked to walk to the middle of the plank and stay in a standing posture above the void with the building behind them. They were asked to stand still during the stimulations and keep their head straight (i.e., not to look down).

Falling from the building (fallingVR).

From the plank, participants were asked to take a large step to their right. The software then simulates a fall of 80 floors. The duration of the fall is 5 s, at a mean speed of 40 m/s. The speed of the fall was progressively increased from the plank to the ground. Once the ground is reached, the screen rapidly fades out to white, and the participant is standing in the street at the starting point, in front of the elevator.

Controlled falling from the building (controlledVR).

From the elevator at the top of the building, participants were asked to grab the hand reactors and fly off the building. Once stabilized at the level of the plank, they were asked to fly downward to the ground with the jet packs, by pressing the appropriate button on the controllers. The duration of the descent was matched to that of the free fall from the plank, i.e., 5 s.



The myoelectrical activity of the triceps surae muscles, as well as head and leg movements were measured throughout the experiment. In each condition, participants were asked to avoid head movements to minimize the influence of head rotations on the corticospinal track (33). In each condition, a total of 10 H-reflexes and 4 maximal muscle action potentials (M-waves) were recorded. At the end of the experiment, participants were asked to indicate the level of fear they felt during the whole session during the falls, on a visual analog scale of 15 cm (from 0 at the left end, corresponding to no fear at all, to 15 at the right end, corresponding to intense panic).

Myoelectrical Activity

Electromyographic signals (EMG) of the right calf muscles were continuously recorded throughout the experiment. The activity was recorded from two muscles of the triceps surae, the soleus (SOL and the medialis gastrocnemius (MG), and from one muscle of the anterior tibial compartment (tibialis anterior, TA). The skin was first shaved and rubbed with alcohol to ensure low impedance ($<5 \text{ k}\Omega$). Trigno sensors (Delsys, Natick, MA) were firmly strapped to the leg using the specially designed adhesive interfaces. Sensors were positioned 2 cm below the insertions of the gastrocnemii over the Achilles tendon for SOL, and over the midbelly of the gastrocnemii muscles for MG (34). Tibialis anterior EMG activity was also recorded by placing the sensor at 1/ 3rd of the distance on the line between the fibula and the tip of the medial malleolus (34). This also helped to ensure a lack of inadvertent TA activation during posterior tibial nerve stimulation.

EMG signals were amplified with a bandwidth frequency ranging from 0.3 Hz to 1 kHz and simultaneously recorded on a computer at a sampling frequency of 2 kHz using the PowerLab data acquisition system (LabChart 8, ADInstruments, Sydney, Australia).

Tibial Nerve Stimulation

Single rectangular pulses (1 ms width) were delivered to the posterior tibial nerve with a constant current (Digitimer DS7, Hertfordshire, UK) to evoke H-reflexes and M-waves of the triceps surae muscles. A self-adhesive cathode (8 mm diameter, Ag-AgCl) was placed in the popliteal fossa and an anode (5 \times 10 cm, Medicompex SA, Ecublens, Switzerland) was placed over the patella. Once the optimal stimulation site providing the greatest response peak-to-peak amplitude was located, the stimulation electrode was fixed firmly with straps to ensure consistency of the responses (35). The intensity of stimulation was then progressively increased from SOL and MG H-reflexes threshold by 2 mA increments to maximal H-reflex (H_{MAX}) and then by 5 mA increments until the M wave of the two muscles no longer increased. This last stimulation intensity was then increased by 20% to ensure supramaximal stimulation and was used to record maximal M wave (M_{MAX}) , so that no variation in M-wave amplitude could be due to variation of axonal excitability (36).

Two intensities were retained from this initial checking: H_{MAX} and M_{MAX} . Responses were evoked during the different conditions with a minimum interval of 4 s and a maximal interval of 10 s. These intervals were chosen to avoid a

potential influence of homo-synaptic postactivation depression from one stimulus to the following one, a minimal interval of 4 s being recommended (37). In addition to the randomization of condition order, several minutes of rest were observed in-between conditions, ensuring no contamination of the results from one condition to another. In each condition (no VR, ground VR, plank VR, falling VR, and jetpack VR), 10 H_{MAX} and four M_{MAX} were evoked. For falling VR, five falls were simulated during which two H-reflexes were evoked 4 s apart, and two falls during which two M_{MAX} were evoked. Similarly, given the duration of the fall, several descents were required in jetpack VR to obtain 10 H_{MAX} and 2 M_{MAX} . H-reflexes and M-waves were evoked in random order during each condition.

Head and Leg Movements

Head movements were accounted for by means of a sensor (Delsys, Natick, MA) placed on the forehead that recorded angular velocity in the three axes (x, y, z) at a frequency of 2,000 Hz. A similar sensor was placed on the leg, at the level of the soleus muscle. Leg and head movements were recorded throughout the experiments to account for different body oscillations among the VR conditions.

Data Analysis

For each muscle and condition, the average peak-topeak amplitudes of the 10 H_{MAX} and the two M_{MAX} were calculated. Average H_{MAX} was normalized to the average M_{MAX} evoked in the same condition ($H_{\text{MAX}}/M_{\text{MAX}}$). The small M-waves accompanying the maximal H-wave $(M_{\rm atH})$ were also measured and normalized by the corresponding maximal M-wave $(M_{\rm atHMAX}/M_{\rm MAX})$. Variations in such responses are useful to identify any modification in posterior tibial nerve stimulation during the experiment (38). In each condition, the root mean square (RMS) of EMG activities of the three muscles (SOL, MG, TA) was calculated over 500 ms windows preceding each stimulation. All RMS of each condition were then averaged and normalized by the corresponding M_{MAX} (RMS/ M_{MAX}). Head and leg movements were both analyzed in the same way, i.e., by calculating the resultant angular velocity among the three axes. The mean value of the 500 ms before each stimulation was evaluated and averaged among the different stimulations of a same condition. These measures were useful to check for possible changes in the initial conditions where each of the H- and M- responses were evoked among the different VR situations.

The % of change in $H_{\text{MAX}}/M_{\text{MAX}}$ from No VR to Falling VR was plotted against the results of the visual analog scale of fear. This latter was calculated as the distance from the mark at the left end of the scale, in mm.

A deeper analysis of data was performed in the falling condition (falling VR) by analyzing separately the five averaged H_{MAX} evoked during the five simulated falls, to account for a potential habituation effect. Responses of the five falls were expressed as a percentage of the first fall. Finally, a separate analysis of the responses of the two stimulations of falling VR was performed, i.e., the response evoked at the beginning of the fall and that evoked immediately before impact with the ground.

Statistical Analysis

All data are presented as means ± standard deviation (SD). The normality of the data was verified using the Shapiro–Wilk test and the homogeneity of variance by the Levene test. As all of the variables followed a Normal distribution, parametric one-way repeated-measures ANOVA was performed on head rotations, leg rotations, TA RMS, SOL, and GM H_{MAX}/M_{MAX} , M_{MAX} amplitude, M_{atH}/M_{MAX} , RMS/ M_{MAX} with the factor "condition" (no VR, ground VR, plank VR, falling VR, jetpack VR). A Bonferroni correction for post hoc analysis was performed with the maximal number of variables tested at the same time for each condition, e.g., M_{MAX} , H_{MAX} , and M_{atH} , leading to a threshold of P = 0.017.

For responses analyzed during the falling VR condition, one-way repeated-measures ANOVA was performed on the responses of the five falls with the factor "fall number" (from one to five). To assess potential differences in H-reflexes evoked at different timepoints during the fall, a two-tailed paired *t* test was performed between the first stimulation at the beginning of the fall (FALL 1) and the second when approaching the ground (FALL 2). Pearson's correlation coefficient was used to assess the correlation between the % change in $H_{\text{MAX}}/M_{\text{MAX}}$ from no VR to falling VR, and the results of the visual analog fear scale, with *P* obtained in the Bravais-Pearson table.

Statistical analysis was performed using STATISTICA (10.0 version, Statsoft, Tulsa, OK). The level of statistical significance was set at P < 0.05.

RESULTS

Initial Check

No effect of the condition was found on normalized background myoelectrical activity (RMS/M_{MAX}) for the SOL

 $(F_{4,56} = 1.067, P = 0.381, \eta_P^2 = 0.071)$, GM $(F_{4,56} = 1.263, P = 0.295, \eta_P^2 = 0.082)$, or TA (RMS only, $F_{4,56} = 1.729, P = 0.156, \eta_P^2 = 0.109)$. No difference was found in head rotations between the different conditions $(F_{3,42} = 1.116, P = 0.353, \eta_P^2 = 0.073)$. Furthermore, leg angular velocity did not vary between conditions $(F_{4,56} = 1.067, P = 0.381, \eta_P^2 = 0.071)$.

Spinal Excitability

In the SOL muscle, a significant effect of the "condition" factor was found on $H_{\text{MAX}}/M_{\text{MAX}}$ ratios ($F_{4,56} = 7.170$, P < 0.001, $\eta_{\text{P}}^2 = 0.34$). $H_{\text{MAX}}/M_{\text{MAX}}$ was significantly lower during falling VR as compared with NoVR (P < 0.001), GroundVR (P = 0.006), and PlankVR (P = 0.013) (Fig. 2). No effect was observed on raw maximal M waves, i.e., M_{MAX} ($F_{4,56} = 1.594$, P = 0.188, $\eta_{\text{P}}^2 = 0.10$), or on normalized submaximal M waves, i.e., $M_{\text{atH}}/M_{\text{MAX}}$ ($F_{4,56} = 0.645$, P = 0.633, $\eta_{\text{P}}^2 = 0.044$).

In the GM muscle, no effect of the "condition" factor was found on any of the neurophysiological indices, i.e., $H_{\text{MAX}}/M_{\text{MAX}}$ ($F_{4,56} = 0.549$, P = 0.701, $\eta_{\text{P}}^2 = 0.038$), M_{MAX} ($F_{4,56} = 2.368$, P = 0.065, $\eta_{\text{P}}^2 = 0.145$) and $M_{\text{atH}}/M_{\text{MAX}}$ ($F_{4,56} = 0.352$, P = 0.841, $\eta_{\text{P}}^2 = 0.025$) (Fig. 3).

Fine Analysis of H-Reflex during Falling

When analyzing responses fall by fall (Fig. 4), no significant differences were found between normalized responses (SOL: $F_{4,56} = 1.549$, P = 0.201, $\eta_P^2 = 0.099$; GM: $F_{4,56} = 0.948$, P = 0.443, $\eta_P^2 = 0.063$). During falling VR, the SOL H-reflex increased significantly (P = 0.006) from the beginning of the fall (FALL 1) and the end (FALL 2) when approaching the ground (Fig. 3). However, no difference was found for SOL H-reflexes in jetpack VR between different stimulation times, whether it was at the beginning of the descent or close to the ground (P =0.329). No difference was observed in GM H-reflexes in



Figure 2. Typical recordings of soleus H-reflexes in the different virtual situations. Each trace is an average of 10 traces. The vertical arrows indicate the moment of stimulation. VR, virtual reality.



Figure 3. H-reflexes during the different virtual situations. A: soleus (SOL) H_{MAX}/M_{MAX} , myoelectrical activity (root mean square, RMS/ M_{MAX}), maximal (M_{MAX}), and submaximal (M_{atH}/M_{MAX}) during the several conditions; B: gastrocnemius (GM) H_{MAX}/M_{MAX} myoelectrical activity (RMS/ M_{MAX}), maximal (M_{atH}/M_{MAX}) during the several conditions. Gray lines represent individual data. *P < 0.05 and **P < 0.01.

any falling situation (P = 0.233). It must be noticed that background EMG activities of SOL did not significantly vary (P = 0.852) from FALL 1 (RMS/ $M_{MAX} = 0.0147 \pm 0.004$) to FALL 2 (RMS/ $M_{MAX} = 0.0146 \pm 0.005$), similarly for GM (FALL1: RMS/ $M_{MAX} = 0.0148 \pm 0.007$; FALL2: RMS/ $M_{MAX} = 0.0145 \pm 0.006$; P = 0.695) and TA (FALL1: RMS = 0.098 ± 0.071 mV; FALL2: RMS = 0.087 ± 0.092; P = 0.281).

A significant correlation was observed between the % change in SOL $H_{\text{MAX}}/M_{\text{MAX}}$ from No VR to Falling VR, and the results of the visual analog fear scale (r = 0.676, P < 0.01) (Fig. 4). No correlation was found for the GM muscle (r = 0.173, P > 0.10). No correlation with VAS was either found for any other condition (change from rest to groundVR, plankVR, jetpackVR).

DISCUSSION

This study investigated the effect of different posturechallenging tasks, simulated using VR, on standing spinal excitability of the triceps surae muscles. The main results illustrate a drastic decrease in H-reflex amplitude of the soleus muscle during falling (fall VR and jetpack VR) compared with quiet standing conditions, while it remained unchanged in the GM muscle. A deeper analysis of soleus H-reflex modulation during the simulated fall revealed that the H-reflex was lower in the first phase of the fall, then increased again slightly in the second phase, i.e., immediately before impact with the ground. These modulations were observed in the absence of any other neuromuscular



Figure 4. In-depth analysis of H-reflexes during virtual falling. *A*: soleus (SOL) and gastrocnemius medialis (GM) H-reflex variation from the first to the fifth virtual fall. Responses are expressed in percentage of the first fall. *B*: relationship between the decrease of H-reflex from virtual falling to the standing quiet condition (in %) and the score of fear on the visual analog scale (VAS). *C*: differences between SOL and GM first H-reflex response at the beginning of the fall (FALL 1) and the second response right before ground contact (FALL 2). **P < 0.01.

modulation (RMS and M-waves) or body movements (head and leg) during the VR conditions.

In real conditions, the H-reflex of the triceps surae muscles, and especially the soleus, is known to be downmodulated with increased complexity of the postural task. Indeed, soleus spinal excitability has been shown to decline from lying down to standing (25, 39), and even from quiet standing to standing on an unstable surface (40). One of the main reasons put forward to explain this is the need for the system to reduce postural sways and prevent overreaction of the plantar flexors, major actors of postural stability, due to large reflexive contractions. This phenomenon is highlighted when participants are standing on a reduced surface (41), and even more so if this reduced base of support is above the ground, such as on a beam (27). For most of these authors, the involvement of spinal presynaptic inhibitory structures seemed to play a major role in the reduction of spinal excitability with the increase in postural challenge (39). This was first attributed to different amplitudes of postural sway, leading to different muscle stretches (soleus) and, per se, different muscle spindle activity, which mediates Ia afferent discharge. Indeed, different postural sways could modulate the amplitude of the H-reflex, due to variations in spindle afferent feedback, which modulates presynaptic inhibition

of Ia afferents (42). However, here, no differences in body movement, as shown by head movement and more particularly, leg angular velocity, was found among the different VR conditions. This result may rule out potential different influence of spindles activity, i.e., mediating Ia afferent discharges, among VR conditions. The changes observed here may then more likely arise from supraspinal influences on spinal circuitry.

It should be noted that spinal networks, especially the presynaptic circuitry, are widely under the influence of supraspinal input (43). Indeed, previous research has shown that presynaptic circuitry can be influenced even by small descending command in the absence of significant modulations of motor output, i.e., background EMG activity. This was shown by motor imagery, i.e., mental simulation of movements (44) or, to a lesser extent, by observation of actions performed by others (45). It was postulated that the effects of vision and posture on spinal excitability of the postural muscles are not necessarily interrelated. Indeed, while both an increase in postural complexity (from two-legged to one-legged standing posture) and a decrease in visual cues (from eyes open to eyes closed) led to a decrease in soleus H-reflex, no interactive effect was observed (46). This emphasizes that H-reflex can be modulated in standing posture by varying visual cues in the absence of balance variations. The lack of difference of background muscle activity in the considered muscles (SOL, GM) also raised potential similar muscle feedbacks. Similarly, the lack of change in antagonist muscle (TA) activity between VR conditions rules out a potential role of co-activation and its associated mechanisms in the observed changes.

Independently of afferent feedback from muscle spindles, visual information delivered by VR was shown to be an important stressor for postural stability and an interesting model to study the importance of visual input on the neuromuscular system that mediates balance (47). Although there is no previous literature specifically on the effect of VR on standing H-reflex, it is known that a complex visual environment could lessen the amplitude of the H reflex (48), i.e., with multiple visual stimuli as compared with absence of stimuli (eyes closed). In the present experiment, the simple fact of being in VR cannot solely explain these results, since no differences were found between rest H-reflex and simple VR tasks (ground VR, plank VR). Interestingly, although of lesser magnitude, jetpack VR also led to a decrease in Hreflexes, as during free falling (falling VR). This meant that H-reflexes were modulated downward both in controlled and uncontrolled falling. These results underline the importance of visual stream during falling, whether the participant can control such a long fall (80 floors) or not.

Moreover, the influence of vestibulo-spinal tract on the triceps surae H-reflex, a main actor of drop landing and balance, has been suggested (49). Indeed, it is now accepted that the vestibular system is able to modulate the cortical output to spinal networks, thus leading to changes in spinal excitability, especially on the triceps surae during standing (49). Using an elegant experimental design with a chair suspended by electromagnets that could induce unexpected falling, Lacour et al. (50) showed that labyrinthectomized monkeys (removal of part of the vestibular system) lose the downward modulation of reflexes during falling. This highlights the important role the vestibular system plays in the modulation of H-reflexes during standing and falling. However, its effects are related to the detection of acceleration by the semicircular canals or otoliths, parts of the vestibular system that are sensitive to body tilt or accelerations. It has been reported that in a quiet standing position, postural oscillations are not sufficient to activate reflex modulation by the vestibular system (51). This rules out a potential influence of direct involvement of the vestibular system in the present experiment, since no differences were found in head movements between VR conditions. However, it is acknowledged that the visual and vestibular systems influence each other. Consequently, visual cues, such as during gaze-stabilization exercises, may influence the vestibulospinal system and lead to a different modulation of triceps surae H-reflex in the standing condition (52). Vestibulo-spinal tracks are also widely influenced by cerebellum networks, at the level of the brainstem (53). Furthermore, the cerebellum could also play a key role in modulating spinal excitability during virtually simulated movements. Important activation of functional circuits within the cerebellum has been illustrated with functional magnetic imagery, during both motor (i.e., in the presence of afferent feedback) or cognitive spatial navigation (54). Therefore, even in the absence of significant changes in muscle afferent feedbacks and/or in head movements that could differently activate vestibular sensors, here, the influence of the vestibulo-spinal tracks on spinal excitability cannot totally be ruled out, although indirectly activated by visual information of falling.

A difference was noted between controlled (jetpack VR) and uncontrolled falling (falling VR) when analyzing the Hreflex responses during falling in greater depth. Indeed, although the H-reflex depression was lower in controlled as compared with uncontrolled falling, the modulation of Hresponse according to the phase of the descent was absent from the controlled falling. This highlights the fact that the visual stream during the descent is not the only cue that modulates the H-reflex, and that in uncontrolled falling, the modulation of spinal excitability when approaching the ground may stem from other sources, such as an internal representation of free falling that is not present when the participant has the feeling that they can control their descent (by means of a jetpack). This internal representation may generate the fear of falling, which is known to be able to modulate spinal circuitry. In fact, in humans, the modulation of the H-reflex during free falling has been studied for years, yet remains quite controversial in the existing literature, and seems to be an individual behavior (55). It also depends on psychologic factors, the falling being either expected or unexpected in the different studies, or on different falling heights. However, in the present study, participants voluntarily chose the moment to jump off the plank, therefore the fall is expected. Furthermore, the downward regulation of spinal excitability was still observed after several trials of virtually simulated falling and did not lessen from one trial to another. This excluded a potential "surprise" effect and showed that the psychological factor influencing spinal excitability was not linked with a sudden and unique stimulus. Indeed, spinal excitability is also known to be reduced when quietly standing on the edge of a raised platform and that this modulation depends on the height of the platform, revealing that postural anxiety can lead to a reduction in H-reflex (29). In the present study, the effect of height was maximized, therefore participants had to jump from a building of 80-floors, which obviously represented for all participant a situation of extreme risk of injury (or even death). In the absence of different afferent feedbacks from postural muscles, as well as from head rotations, such a decrease in spinal excitability could then be attributed mostly to input from the brain, which responds to a situation of danger. Therefore, the visual cues generated by VR, associated with the feeling of uncontrolled falling, might generate the sensation of actual falling.

The literature about H-reflex variations observed during real falling indicates that VR simulation of free falling seems to mimic the actual modulations. The H-reflex is known to be downmodulated during drop jumps, is inhibited during the aerial phase, and increased immediately before impact (56). This slight increase before ground impact, even though the H-reflex remains lower than the rest response, is to prepare the muscles and the spinal level, which mediates the stretch reflex, to manage the landing, and possibly the rebound (in case of a drop jump). It seems that the neuromuscular system can anticipate the plantar flexor stretch, and more specifically the soleus muscle, for a landing that causes sudden ankle dorsiflexion (57).

It should be noticed that spinal excitability decreases during VR-simulated falling were only observed in soleus muscle (SOL), while it remained unchanged for the gastrocnemius medialis (GM). Although gastrocnemii muscles are synergists to SOL, their respective spinal circuits are not necessarily modulated in the same manner by descending and/or afferent drives (24). Several factors may explain these differences. First, they present different biomechanical configuration and function, gastrocnemii being pluriarticular (also knee flexors), that would lead to different results in their respective H-reflexes (58). Here, this could lead to a methodological issue regarding the fact that in standing posture gastrocnemii muscles are stretched because the leg is fully extended, while to optimize the assessment of gastrocnemii H-reflex it is usually recommended to stimulate with knee bent at 90° (59). In general, the present experimental design regarding participant's posture and stimulation conditions is optimal for the soleus muscle, therefore it remains possible that GM evaluation was slightly underrated. However, several neurophysiological mechanisms may contribute to a larger extent to the differences observed here between SOL and GM. Indeed, it is known that spinal circuitry is different between these two muscles, leading them to respond differently to some interventions (60). This difference is mainly a result of their different type of motor units, i.e., slow (SOL) versus fast (GM) (61) or their difference in muscle spindles density that mediate the stretch reflex, being higher in SOL than in GM (58). It is acknowledged that low-threshold slow motoneurons are more prone to depression, whereas high-threshold fast motoneurons are less sensitive to inhibition (62, 63). Moreover, presynaptic inhibition may be differently controlled by the descending inputs in gastrocnemii and in SOL motoneuronal pools (64). Particularly, vestibulo-spinal projections may exhibit differences from gastrocnemii to soleus muscles (65). These differences may arise from a slight different functional role in balance, SOL being constantly active while gastrocnemii operate to correct transient disturbances (66-68). Therefore, in the present study, the differences observed between GM and SOL H-reflex behavior during VR could be due to several factors, from methodological concerns to intrinsic muscles composition, and more importantly to different cortico-spinal projections and influences. The different origins of this difference are not possible to distinguish with the current results, and especially if this difference in VR is the sole result of different cortical influences. A specific rationale aiming at isolating GM to SOL corticospinal projections, for instance with transcranial magnetic conditioning or with corticomuscular coherences analysis (EEG-EMG) could help address this question.

Finally, a significant correlation has been observed from the score to the visual scale of fear and the SOL H-reflex downregulation during falling. No correlation has been observed between this score and the other condition, especially with controlled falling (jetpack VR). Once again, this highlights a potential link between the spinal mechanisms activated during falling and psychological factors. However, the relationships observed showed that H-reflex was less modulated as the VAS score of fear was high. The direction of this relationship could be interpreted as an inhibition of the motor system processes according to the level of fear. Therefore, such psychological factors could lead to a downregulation of the actual mechanism that could be observed in real drop landing, because of the unusual and stressful situation experienced here in VR. This assumption necessitates further investigation to be ascertained but shows that this first study opens interesting tracks for future research.

Practical Implications

It can be noted that the position in which participants performed VR also contributed to the effect, the standing posture being closer to the simulated situation. Indeed, background muscle activity induced by the standing posture accounts less for H-reflex modulation than the body position itself (24). This highlights the importance of body position on spinal modulations and underlines that the combination with visual feedback provided by VR may provide better results, although this needs to be confirmed. Therefore, the use of multi-sensorial stimulation, which includes visual information through VR and peripheral sensory information that matches the simulated simulation, can be recommended to maximize the effect of VR in a clinical setup.

In fact, most studies on VR in the literature have focused on virtual contexts unrelated to voluntary movements, such as the roller coaster situation (69). Thus, the use of virtual contexts close to human motor activity could lead to significant gains if this modality is used in sports training or in rehabilitation. Indeed, the important psychological and physiological stimulation, possibly associated with the activation of the sensorimotor system, could enable the creation of a context favorable to increases in performance when VR is used in a chronic approach. In addition, the present results showed that the effect observed lasted over the first VRsimulated falling with no change over the several trials (7 simulated falling here), excluding the "surprise" effect of the first trial. This raises a potential effect of such VR protocol over a longer exposure, therefore being potentially beneficial for patients whose spinal circuitry is particularly affected such as those with spasticity (70), chronic ankle instability (71), amyotrophic lateral sclerosis (72), and evidently spinal cord injury (73). In these cases, the present study shows that VR offers the opportunity to solicitate spinal mechanisms associated to posture with a minimal physical stress as compared with traditional gait exercises.

Study Limitation

In the present study, the maximal H-reflex has been used as the marker of spinal excitability, normalized by the maximal M-wave (H_{MAX}/M_{MAX}). It is known that H_{MAX} may not represent the optimal intensity for such exploratory study where there could be both a facilitation and an inhibition, especially for facilitation because of a potential ceiling effect. To that aim, some previous experiments used a lower H-reflex stimulation intensity, for instance, the one evoking 50% of maximal H-reflex. This intensity ensures susceptibility to both facilitation and/or inhibition (39, 74). In fact, the ideal experimental design would be to evoke two or more different H-reflex intensities, lying on the ascending part of the H-reflex recruitment curve (38), which also allows to account for the "size-effect" especially when it is about measuring an inhibition. However, in the present study, this would have led to multiplying the number of trials and therefore performing multiple times more the VR conditions. This could have represented a limitation, both for the observed effects

and for the acceptance of participants. As the H-reflex could be of relatively small amplitude in a standing posture for some participants, maximal H-reflex intensity has been chosen to warrant a sufficient initial size. While at rest and in relaxed conditions (i.e., in sitting position and with no background muscle activity), the ceiling effect of H_{MAX} could be easily reached, in standing posture (as in the present study) the state of the Ia- α motoneuron synapse would allow to still observe upward modulations. Indeed, maximal H-reflex is decreased from sitting to standing (24). This is not explained by different stimulation conditions from sitting to standing but by a different level of presynaptic inhibition of Ia afferent terminals onto the α motoneurons, which mechanisms are highly dependent upon descending inputs (39). In any case, the present study represents a first step toward a deeper understanding of spinal excitability changes with such VR intervention. Further experiments are warranted with various H-reflex intensities, but also with conditioning maneuvers (e.g., D1 presynaptic inhibition), to decipher the underlined balance between facilitation and inhibition.

In the present study, anxiety related to simulated falling was only assessed through a global visual scale asked at the end of the experiment. To deepen the analysis on the relationship between spinal changes and the sensation of fear, participants could have been asked to rate their perception after each of the situations. This would also have helped in understanding a possible acclimatization effect in response to the repetition of VR situations. However, the randomization process of the present study, from one condition to another and from one parameter to another (H-reflex and M-wave) would have led to a complex analysis of the order effect. In complement, such scale is eminently subjective, while other markers of stress could also be tracked concomitantly with corticospinal changes. Indeed, other VR situations were shown to change objective markers of stress, i.e., heart rate variability (75) or in skin conductance (76). These markers are, however, more difficult to analyze when the participant is not in totally quiet position, like in the present study where participants were standing and moving in the virtual environment. Further experiments are then warranted to objectify in realtime the stress induced by such VR conditions and analyze its relationship with neuromuscular modulations.

Conclusions and Perspectives

Visual simulation of free falling induced by VR was sufficient to induce spinal excitability changes mimicking those observed during actual falling. This was observed even in the absence of other peripheral input, since no change was observed in head and leg movements, or in background EMG activity of the plantar flexors. However, this effect seems to be targeted to the muscles most involved in posture, since the GM remained unaffected, contrary to the SOL, which is a main antigravity muscle.

For patients as for athletes, VR could thus make it possible to work as closely as possible to the conditions of the desired performance (replication of a real situation), while maintaining the person in safe conditions. There is currently no literature on the use of VR in a training context and its effects on the neuromuscular system such as the spinal excitability. The present results represent a very promising first step toward further research on corticospinal circuitry modulation induced by VR. For example, testing in more detail the relationship between neuromuscular system adaptation and perception of risk can be the next step. In the present case, testing the effect of different simulated falling heights that represent different levels of risk according to the participant, could be an interesting track for further studies. Furthermore, investigating the relationship between neuromuscular mechanisms and stress/anxiety generated by VR could also represent a very interesting track to follow.

DATA AVAILABILITY

Data will be made available upon reasonable request.

GRANTS

This work was funded by the program "Chrysalide" of the University of Franche-Comté.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.G. conceived and designed research; S.G., P.E. and P.-M.M. performed experiments; S.G. analyzed data; S.G., P.E., and P.-M.M. interpreted results of experiments; S.G. prepared figures; S.G., P.E., and P.-M.M. drafted manuscript; S.G., P.E., and P.-M.M. edited and revised manuscript; S.G., P.E., and P.-M.M. approved final version of manuscript.

REFERENCES

- Carvalho KN, Pearlson GD, Astur RS, Calhoun VD. Simulated driving and brain imaging: Combining behavior, brain activity, and virtual reality. CNS Spectr 11: 52–62, 2006. doi:10.1017/s1092852900024214.
- Feitosa JA, Fernandes CA, Casseb RF, Castellano G. Effects of virtual reality-based motor rehabilitation: a systematic review of fMRI studies. J Neural Eng 19:1, 2022. doi:10.1088/1741-2552/ac456e.
- Gao Y, Ma L, Lin C, Zhu S, Yao L, Fan H, Gong J, Yan X, Wang T. Effects of virtual reality-based intervention on cognition, motor function, mood, and activities of daily living in patients with chronic stroke: a systematic review and meta-analysis of randomized controlled trials. *Front Aging Neurosci* 13: 766525, 2021. doi:10.3389/ fnagi.2021.766525.
- August K, Lewis JA, Chandar G, Merians A, Biswal B, Adamovich S. fMRI analysis of neural mechanisms underlying rehabilitation in virtual reality: activating secondary motor areas. *Conf Proc IEEE Eng Med Biol Soc* 2006: 3692–3695, 2006. doi:10.1109/IEMBS.2006.260144.
- Hao J, Xie H, Harp K, Chen Z, Siu KC. Effects of virtual reality intervention on neural plasticity in stroke rehabilitation: a systematic review. Arch Phys Med Rehabil 103: 523–541, 2022. doi:10.1016/j. apmr.2021.06.024.
- Mekbib DB, Debeli DK, Zhang L, Fang S, Shao Y, Yang W, Han J, Jiang H, Zhu J, Zhao Z, Cheng R, Ye X, Zhang J, Xu D. A novel fully immersive virtual reality environment for upper extremity rehabilitation in patients with stroke. *Ann N Y Acad Sci* 1493: 75–89, 2021. doi:10.1111/nyas.14554.
- Mekbib DB, Zhao Z, Wang J, Xu B, Zhang L, Cheng R, Fang S, Shao Y, Yang W, Han J, Jiang H, Zhu J, Ye X, Zhang J, Xu D. Proactive motor functional recovery following immersive virtual reality-based limb mirroring therapy in patients with subacute stroke. *Neurotherapeutics* 17: 1919–1930, 2020. doi:10.1007/s13311-020-00882-x.
- Prochnow D, Bermúdez I Badia S, Schmidt J, Duff A, Brunheim S, Kleiser R, Seitz RJ, Verschure PFMJ. A functional magnetic resonance imaging study of visuomotor processing in a virtual reality-

based paradigm: rehabilitation gaming system. *Eur J Neurosci* 37: 1441–1447, 2013. doi:10.1111/ejn.12157.

- Gentilucci M, Fogassi L, Luppino G, Matelli M, Camarda R, Rizzolatti G. Functional organization of inferior area 6 in the macaque monkey. I. Somatotopy and the control of proximal movements. *Exp Brain Res* 71: 475–490, 1988. doi:10.1007/BF00248741.
- Modroño C, Navarrete G, Rodríguez-Hernández AF, González-Mora JL. Activation of the human mirror neuron system during the observation of the manipulation of virtual tools in the absence of a visible effector limb. *Neurosci Lett* 555: 220–224, 2013. doi:10.1016/ j.neulet.2013.09.044.
- Djebbara Z, Fich LB, Petrini L, Gramann K. Sensorimotor brain dynamics reflect architectural affordances. *Proc Natl Acad Sci USA* 116: 14769–14778, 2019. doi:10.1073/pnas.1900648116.
- Servotte JC, Goosse M, Campbell SH, Dardenne N, Pilote B, Simoneau IL, Guillaume M, Bragard I, Ghuysen A. Virtual reality experience: immersion, sense of presence, and cybersickness. *Clin Simul Nurs* 38: 35–43, 2020. doi:10.1016/j.ecns.2019.09.006.
- Hudson S, Matson-Barkat S, Pallamin N, Jegou G. With or without you? Interaction and immersion in a virtual reality experience. *J Bus Res* 100: 459–468, 2019. doi:10.1016/j.jbusres.2018.10.062.
- Jang S, Vitale JM, Jyung RW, Black JB. Direct manipulation is better than passive viewing for learning anatomy in a three-dimensional virtual reality environment. *Comput Educ* 106: 150–165, 2017. doi:10.1016/ j.compedu.2016.12.009.
- Marchal V, Sellers J, Pélégrini-Issac M, Galléa C, Bertasi E, Valabrègue R, Lau B, Leboucher P, Bardinet E, Welter ML, Karachi C. Deep brain activation patterns involved in virtual gait without and with a doorway: an fMRI study. *PLoS One* 14: e0223494, 2019. doi:10.1371/journal.pone.0223494.
- Sangani S, Lamontagne A, Fung J. Cortical mechanisms underlying sensorimotor enhancement promoted by walking with haptic inputs in a virtual environment. *Prog Brain Res* 218: 313–330, 2015. doi:10.1016/bs.pbr.2014.12.003.
- Morizio C, Billot M, Daviet JC, Baudry S, Barbanchon C, Compagnat M, Perrochon A. Postural control disturbances induced by virtual reality in stroke patients. *Appl Sci* 11: 1510, 2021. doi:10.3390/app11041510.
- Horlings CGC, Carpenter MG, Küng UM, Honegger F, Wiederhold B, Allum JHJ. Influence of virtual reality on postural stability during movements of quiet stance. *Neurosci Lett* 451: 227–231, 2009. doi:10.1016/j.neulet.2008.12.057.
- Luo H, Wang X, Fan M, Deng L, Jian C, Wei M, Luo J. The effect of visual stimuli on stability and complexity of postural control. *Front Neurol* 9: 48, 2018. doi:10.3389/fneur.2018.00048.
- Robert MT, Ballaz L, Lemay M. The effect of viewing a virtual environment through a head-mounted display on balance. *Gait Posture* 48: 261–266, 2016. doi:10.1016/j.gaitpost.2016.06.010.
- Chiarovano E, Wang W, Rogers SJ, MacDougall HG, Curthoys IS, de Waele C. Balance in virtual reality: effect of age and bilateral vestibular loss. Front Neurol 8: 5, 2017. doi:10.3389/fneur.2017.00005.
- Delaux A, de Saint Aubert JB, Ramanoël S, Bécu M, Gehrke L, Klug M, Chavarriaga R, Sahel JA, Gramann K, Arleo A. Mobile brain/body imaging of landmark-based navigation with high-density EEG. *Eur J Neurosci* 54: 8256–8282, 2021. doi:10.1111/ejn.15190.
- Capaday C, Stein RB. Difference in the amplitude of the human soleus H reflex during walking and running. *J Physiol* 392: 513–522, 1987. doi:10.1111/j.1469-7793.1999.929ab.x.
- Cattagni T, Martin A, Scaglioni G. Is spinal excitability of the triceps surae mainly affected by muscle activity or body position? J Neurophysiol 111: 2525–2532, 2014. doi:10.1152/jn.00455.2013.
- Koceja DM, Markus CA, Trimble MH. Postural modulation of the soleus H reflex in young and old subjects. *Electroencephalogr Clin Neurophysiol Electromyogr* 97: 387–393, 1995. doi:10.1016/0924-980x(95)00163-f.
- Tokuno CD, Taube W, Cresswell AG. An enhanced level of motor cortical excitability during the control of human standing. *Acta Physiol* (*Oxf*) 195: 385–395, 2009. doi:10.1111/j.1748-1716.2008.01898.x.
- Llewellyn M, Yang JF, Prochazka A. Human H-reflexes are smaller in difficult beam walking than in normal treadmill walking. *Exp Brain Res* 83: 22–28, 1990. doi:10.1007/BF00232189.
- McIlroy WE, Bishop DC, Staines WR, Nelson AJ, Maki BE, Brooke JD. Modulation of afferent inflow during the control of balancing tasks using the lower limbs. *Brain Res* 961: 73–80, 2003. doi:10.1016/ s0006-8993(02)03845-3.

- Sibley KM, Carpenter MG, Perry JC, Frank JS. Effects of postural anxiety on the soleus H-reflex. *Hum Mov Sci* 26: 103–112, 2007. doi:10.1016/j.humov.2006.09.004.
- Horslen BC, Murnaghan CD, Inglis JT, Chua R, Carpenter MG. Effects of postural threat on spinal stretch reflexes: evidence for increased muscle spindle sensitivity? *J Neurophysiol* 110: 899–906, 2013. doi:10.1152/jn.00065.2013.
- Cleworth TW, Horslen BC, Carpenter MG. Influence of real and virtual heights on standing balance. *Gait Posture* 36: 172–176, 2012. doi:10.1016/j.gaitpost.2012.02.010.
- Grosprêtre S, Marusic U, Gimenez P, Ennequin G, Mourot L, Isacco L. Stand up to excite the spine: neuromuscular, autonomic, and cardiometabolic responses during motor imagery in standing vs. sitting posture. *Front Physiol* 12: 1–19, 2021. doi:10.3389/fphys.2021. 762452.
- Schieppati M. The Hoffmann reflex: a means of assessing spinal reflex excitability and its descending control in man. *Prog Neurobiol* 28: 345–376, 1987. doi:10.1016/0301-0082(87)90007-4.
- Hermens HJ, Freriks B, Disselhorst-Klug C, Rau G. Development of recommendations for SEMG sensors and sensor placement procedures. J Electromyogr Kinesiol 10: 361–374, 2000. doi:10.1016/ s1050-6411(00)00027-4.
- Cattagni T, Merlet AN, Cornu C, Jubeau M. H-reflex and M-wave recordings: effect of pressure application to the stimulation electrode on the assessment of evoked potentials and subject's discomfort. *Clin Physiol Funct Imaging* 38: 416–424, 2018. doi:10.1111/ cpf.12431.
- Kiernan MC, Lin CS-Y, Burke D. Differences in activity-dependent hyperpolarization in human sensory and motor axons. *J Physiol* 558: 341–349, 2004. doi:10.1113/jphysiol.2004.063966.
- Stein RB, Estabrooks KL, McGie S, Roth MJ, Jones KE. Quantifying the effects of voluntary contraction and inter-stimulus interval on the human soleus H-reflex. *Exp Brain Res* 182: 309–319, 2007. doi:10.1007/s00221-007-0989-x.
- Grosprêtre S, Martin A. H reflex and spinal excitability: methodological considerations. *J Neurophysiol* 107: 1649–1654, 2012. doi:10.1152/ jn.00611.2011.
- Katz R, Meunier S, Pierrot-Deseilligny E. Changes in presynaptic inhibition of ia fibres in man while standing. *Brain* 111: 417–437, 1988. doi:10.1093/brain/111.2.417.
- Chalmers GR. Modulation of tendon tap reflex activation of soleus motor neurons with reduced stability tandem stance. *Hum Mov Sci* 64: 274–282, 2019. doi:10.1016/j.humov.2019.02.013.
- Trimble MH, Koceja DM. Effect of a reduced base of support in standing and balance training on the soleus H-reflex. *Int J Neurosci* 106: 1–20, 2001. doi:10.3109/00207450109149734.
- Trimble MH. Postural modulation of the segmental reflex: effect of body tilt and postural sway. *Int J Neurosci* 95: 85–100, 1998. doi:10.3109/00207459809000652.
- Pierrot-Deseilligny E, Burke D. The Circuitry of the Human Spinal Cord: Its Role in Motor Control and Movement Disorders. Cambridge, UK: Cambridge University Press, 2005.
- Grosprêtre S, Lebon F, Papaxanthis C, Martin A. Spinal plasticity with motor imagery practice. *J Physiol* 597: 921–934, 2019. doi:10.1113/ JP276694.
- Baldissera F, Cavallari P, Craighero L, Fadiga L. Modulation of spinal excitability during observation of hand actions in humans. *Eur J Neurosci* 13: 190–194, 2001. doi:10.1046/j.0953-816x.2000.01368.x.
- Pinar S, Kitano K, Koceja DM. Role of vision and task complexity on soleus H-reflex gain. J Electromyogr Kinesiol 20: 354–358, 2010. doi:10.1016/j.jelekin.2009.03.002.
- Moscatelli F, Valenzano A, Petito A, Triggiani AI, Ciliberti MAP, Luongo L, Carotenuto M, Esposito M, Messina A, Monda V, Monda M, Capranica L, Messina G, Cibelli G. Relationship between blood lactate and cortical excitability between taekwondo athletes and non-athletes after hand-grip exercise. *Somatosens Mot Res* 33: 137– 144, 2016. doi:10.1080/08990220.2016.1203305.
- Earles DR, Koceja DM, Shively CW. Environmental changes in soleus H-reflex excitability in young and elderly subjects. *Int J Neurosci* 105: 1–13, 2000. doi:10.3109/00207450009003261.
- Nepveu JF, Mikhail Y, Pion CH, Gossard JP, Barthélemy D. Assessment of vestibulocortical interactions during standing in healthy subjects. *PLoS One* 15: e0233843, 2020. doi:10.1371/journal. pone.0233843.

- Lacour M, Xerri C, Hugon M. Muscle responses and monosynaptic reflexes in falling monkey. Role of the vestibular system. *J Physiol* (*Paris*) 74: 427–438, 1978.
- Nashner LM, Shupert CL, Horak FB, Black FO. Organization of posture controls: An analysis of sensory and mechanical constraints. *Prog Brain Res* 80: 411–418, 1989. doi:10.1016/s0079-6123(08)62237-2.
- Matsugi A, Ueta Y, Oku K, Okuno K, Tamaru Y, Nomura S, Tanaka H, Mori N. Effect of gaze-stabilization exercises on vestibular function during postural control. *Neuroreport* 28: 439–443, 2017. doi:10.1097/WNR.00000000000776.
- Miall RC. Systems descending from the brainstem: basic principles: other descending pathways and motor control. In: *Neuroscience in the 21st Century: From Basic to Clinical* (2nd ed.), edited by Pfaff D, Volkow ND. New York: Springer, 2016, p. 1225–1237.
- Iglói K, Doeller CF, Paradis AL, Benchenane K, Berthoz A, Burgess N, Rondi-Reig L. Interaction between hippocampus and cerebellum crus i in sequence-based but not place-based navigation. *Cereb Cortex* 25: 4146–4154, 2015. doi:10.1093/cercor/bhu132.
- Greenwood R, Hopkins A. Monosynaptic reflexes in falling man. J Neurol Neurosurg Psychiatry 40: 448–454, 1977. doi:10.1136/ jnnp.40.5.448.
- Taube W, Leukel C, Schubert M, Gruber M, Rantalainen T, Gollhofer A. Differential modulation of spinal and corticospinal excitability during drop jumps. *J Neurophysiol* 99: 1243–1252, 2008. doi:10.1152/jn.01118.2007.
- Lyle MA, McLeod MM, Pouliot BA, Thompson AK. Soleus H-reflex modulation during a double-legged drop landing task. *Exp Brain Res* 240: 1093–1103, 2022. doi:10.1007/s00221-022-06316-8.
- Tucker KJ, Tuncer M, Türker KS. A review of the H-reflex and Mwave in the human triceps surae. *Hum Mov Sci* 24: 667–688, 2005. doi:10.1016/j.humov.2005.09.010.
- Merlet AN, Cattagni T, Cornu C, Jubeau M. Effect of knee angle on neuromuscular assessment of plantar flexor muscles: a reliability study. *PLoS One* 13: e0195220, 2018. doi:10.1371/journal.pone.0195220.
- Duclay J, Martin A, Robbe A, Pousson M. Spinal reflex plasticity during maximal dynamic contractions after eccentric training. *Med Sci Sports Exerc* 40: 722–734, 2008. doi:10.1249/MSS.0b013e31816184dc.
- Johnson MA, Polgar J, Weightman D, Appleton D. Data on the distribution of fibre types in thirty-six human muscles. an autopsy study. J Neurol Sci 18: 111–129, 1973. doi:10.1016/0022-510x(73)90023-3.
- Koerber HR, Mendell LM. Modulation of synaptic transmission at laafferent connections on motoneurons during high-frequency afferent stimulation: dependence on motor task. J Neurophysiol 65: 1313–1320, 1991. doi:10.1152/jn.1991.65.6.1313.
- Lev-Tov A. Junctional transmission in fast- and slow-twitch mammalian motor units. J Neurophysiol 57: 660–671, 1987. doi:10.1152/ jn.1987.57.3.660.

- Nielsen J, Kagamihara Y. The regulation of presynaptic inhibition during co-contraction of antagonistic muscles in man. *J Physiol* 464: 575–593, 1993. doi:10.1113/jphysiol.1993.sp019652.
- Dakin CJ, Héroux ME, Luu BL, Inglis JT, Blouin JS. Vestibular contribution to balance control in the medial gastrocnemius and soleus. *J Neurophysiol* 115: 1289–1297, 2016. doi:10.1152/jn.00512.2015.
- Héroux ME, Dakin CJ, Luu BL, Inglis JT, Blouin JS. Absence of lateral gastrocnemius activity and differential motor unit behavior in soleus and medial gastrocnemius during standing balance. J Appl Physiol (1985) 116: 140–148, 2014. doi:10.1152/japplphysiol.00906.2013.
- Vieira TMM, Loram ID, Muceli S, Merletti R, Farina D. Recruitment of motor units in the medial gastrocnemius muscle during human quiet standing: Is recruitment intermittent? what triggers recruitment? J Neurophysiol 107: 666–676, 2012. doi:10.1152/jn.00659.2011.
- Ward SR, Eng CM, Smallwood LH, Lieber RL. Are current measurements of lower extremity muscle architecture accurate? *Clin Orthop Relat Res* 467:1074–1082, 2009. doi:10.1007/s11999-008-0594-8.
- Fadeev KA, Smirnov AS, Zhigalova OP, Bazhina PS, Tumialis AV, Golokhvast KS. Too real to be virtual: autonomic and EEG responses to extreme stress scenarios in virtual reality. *Behav Neurol* 2020: 5758038, 2020. doi:10.1155/2020/5758038.
- Milanov I. Clinical and neurophysiological correlations of spasticity. *Funct Neurol* 14: 193–201, 1999.
- Kim K-M, Kim J-S, Cruz-Díaz D, Ryu S, Kang M, Taube W. Changes in spinal and corticospinal excitability in patients with chronic ankle instability: a systematic review with meta-analysis. J Clin Med 8: 1037, 2019. doi:10.3390/jcm8071037.
- Mazzini L, Balzarini C. An overview of H-reflex studies in amyotrophic lateral sclerosis. *Amyotroph Lateral Scler Other Motor Neuron Disord* 1: 313–318, 2000. doi:10.1080/146608200300079554.
- Korupolu R, Stampas A, Singh M, Zhou P, Francisco G. Electrophysiological outcome measures in spinal cord injury clinical trials: a systematic review. *Top Spinal Cord Inj Rehabil* 25: 340–354, 2019. doi:10.1310/sci2504-340.
- Hultborn H, Meunier S, Morin C, Pierrot-Deseilligny E. Assessing changes in presynaptic inhibition of I a fibres: a study in man and the cat. J Physiol 389: 729–756, 1987. doi:10.1113/jphysiol.1987. sp016680.
- Ham J, Cho D, Oh J, Lee B. Discrimination of multiple stress levels in virtual reality environments using heart rate variability. *Annu Int Conf IEEE Eng Med Biol Soc* 2017: 3989–3992, 2017. doi:10.1109/ EMBC.2017.8037730.
- Liu Q, Zhang W. Sex differences in stress reactivity to the trier social stress test in virtual reality. *Psychol Res Behav Manag* 13: 859–869, 2020. doi:10.2147/PRBM.S268039.