A Fine Balance:
Contextual Modulation in Lower Limb Tactile Sensitivity Under Postural and Motor Demands

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Abstract

Tactile perception in the lower limbs is essential for maintaining balance and coordinating movement. Unlike the upper limbs, where movement errors are often tolerable, failures in posture control can result in instability or falls—particularly in older adults. This cumulative dissertation investigates how lower-limb somatosensory perception adapts to postural and sensorimotor demands, guided by models of predictive coding and reliability-based sensory integration.

Three experimental studies examined changes in vibrotactile perception during (1) quiet stance under stable and unstable conditions in young and older adults, (2) temporally predictable and unpredictable visual perturbations, and (3) goal-directed leg movements involving distinct functional roles of each leg. Across all studies, tactile perception dynamically modulated depending on postural state, task phase, and limb function.

Instability and postural load led to reduced perception, while balance-threatening or feedback-critical phases triggered transient enhancement. Older adults showed elevated baseline thresholds at rest but preserved modulation across postural conditions, suggesting intact compensatory reweighting. This indicates that while sensory degradation occurs with age, adaptive mechanisms remain functionally effective.

These findings support a dynamic model of lower-limb tactile perception, shaped by posture, timing, and behavioral relevance. They also emphasize the functional distinctiveness of the lower limbs, where sensorimotor demands are more tightly coupled to stability and whole-body control than in the upper limbs.

Contents

I. Synopsis

1 Introduction

Imagine a gymnast performing a floor routine. Every step, leap, twist, and hold demands precise motor execution, not only to impress the judges with flawless form, but also to prepare for the next movement and, most importantly, to maintain balance and avoid an uncontrolled fall. Now, imagine if we could visualize the electrical impulses of the human sensorimotor system during this routine. With every ground contact, a rapid burst of activity would ignite in the tactile receptors of the contacting body part, traveling at high speed toward the central nervous system. These signals would reach the brain, making their way through the thalamus and cortical circuits, merging and interacting with other neural inputs, before newly computed motor commands cascade back down toward the muscles, encoding the precise adjustments required for the next action. This seamless loop of perception and action, from skin to brain to muscle, reflects the body's remarkable ability to integrate sensory input and generate motor output.

The human sensorimotor system operates under substantial complexity, integrating high-dimensional sensory input with motor commands across numerous degrees of freedom to produce even a single coordinated movement. Postural control presents a particularly demanding challenge, as it not only requires the continuous integration of multisensory information and the regulation of multiple effectors, but is also associated with a high cost of failure. Compared to upper limb tasks such as reaching or object manipulation, failures in postural control carry substantial biomechanical and health-related risks.

In this work, I present three articles investigating how the human sensorimotor system adapts under varying postural demands, in unstable environments, and across the lifespan. Specifically, I explore sensory perception in the lower limbs during standing on stable versus unstable ground, and compare these processes in young and older adults to understand age-related changes in sensorimotor control. Next, I examine how the perception of a moving room, either predictable or temporally uncertain, influences tactile processing over time. Finally, I investigate the highly dynamic act of kicking, analyzing how tactile integration evolves before, during, and after ball contact in both the kicking and balancing legs. Across all experiments, I discuss the mechanisms that underlie changes in tactile information processing in the lower limbs.

1.1 Tactile perception and movement-related sensory modulation

Tactile perception enables the nervous system to detect and interpret physical contact with the environment. Mechanoreceptors in the skin of the hands and feet transduce indentation, vibration, and skin stretch into neural signals, providing critical information for object manipulation, postural control, and movement coordination (Johansson & Westling, 1984; Voudouris et al., 2019; Assländer et al., 2018; Jeka et al., 2000). While upper-limb touch has been extensively studied in the context of object manipulation and the decrease in perception termed sensory attenuation, tactile input from the lower limbs remains less well understood, despite its central role in detecting ground contact, stabilizing posture, and regulating gait (Kavounoudias et al., 2001; Mouchnino & Blouin, 2013).

Crucially, tactile perception is not fixed but dynamically modulated. One well-known phenomenon is *tactile suppression*, wherein perception of externally applied stimuli is reduced during movement or in anticipation of it (Blakemore et al., 1999; Voss et al., 2008). This suppression is thought to reflect predictive mechanisms that downregulate expected sensory consequences of self-generated actions, helping to distinguish reafferent from exafferent input and to prioritize movement-relevant signals (Kilteni & Ehrsson, 2022). However, suppression is not uniform: depending on the body part, movement phase, and task context, tactile signals may be attenuated, unchanged, or even enhanced (Fraser & Fiehler, 2018; Voudouris & Fiehler, 2021).

In experimental settings, tactile perception is typically assessed via psychophysical detection or discrimination thresholds. Mechanical stimulation methods include sinusoidal vibration (commonly between 10–250 Hz)(Fuehrer et al., 2022; Gescheider et al., 2002), brief pressure pulses (Craig, 1974; Buckingham et al., 2010), or transcutaneous electrical stimulation (Chapman et al., 1987; Cybulska-Klosowicz et al., 2011; Juravle et al., 2018). Detection thresholds serve as behavioral proxies for sensory gain and reflect both peripheral afferent responsiveness (Johansson & Vallbo, 1979) and central processing efficiency (Wolpert & Flanagan, 2001). Vibration frequency is closely linked to receptor selectivity: Meissner corpuscles are most responsive to low-frequency vibration (10–100 Hz), while Pacinian corpuscles are tuned to higher frequencies (~40–800 Hz); Merkel and Ruffini endings encode sustained indentation and skin stretch (Bolanowski et al., 1988). These mechanoreceptive signals ascend via the dorsal column–medial lemniscal pathway to the contralateral primary somatosensory cortex, where information is further processed and integrated with input from other modalities and predictive motor circuits (Hsiao & Gomez-Ramirez, 2012).

Whereas tactile perception in the hands is critical for fine motor movements and object interactions, cutaneous signals from the foot sole contribute to estimating body orientation, detecting perturbations, coordinating stance adjustments, and initiating gait, all while accounting for ongoing postural demands and whole body dynamics (Kavounoudias et al., 1998, 1999; Mouchnino & Blouin, 2013; Mouchnino et al., 2015). Although the same receptor types occur in feet and hands, they seem to have evolved differently in density, distribution, receptive field size, and force thresholds (Inglis et al., 2002; Trulsson, 2001). Compared to the hands, the principles guiding *how and when* tactile input from the feet or legs is modulated remain poorly defined. In particular, it is unclear how postural instability or environmental changes influence tactile gain control in these regions.

Importantly, tactile processing is not only shaped by movement or posture per se, but also by the broader context in which an action is embedded. Sensorimotor demands, such as the relevance, timing, and predictability of sensory events, play a central role in determining whether tactile input is attenuated or enhanced both in the upper (Fraser & Fiehler, 2018; Voudouris et al., 2019; Voudouris & Fiehler, 2021) and lower limbs (Staines et al., 2000). For example, during goal-directed reaching, tactile perception is dynamically modulated across movement phases, with suppression strongest during movement initiation and weakest when tactile feedback is needed for fine-tuned guidance (Juravle et al., 2010; Voudouris & Fiehler, 2021). There are also indications that cognitive load plays a role by reducing tactile perception (McManus et al., 2023). This context dependence extends to postural and whole-body actions: in balance tasks, tactile perception at the leg can increase prior to expected perturbations, suggesting an anticipatory upregulation of relevant input (Mouchnino et al., 2015; Saradjian et al., 2013). Conversely, when afferent load is high, as during strong contact or sudden impact, sensory masking may transiently override fine tactile perception (Abramsky et al., 1971; Kirman, 1984; Williams & Chapman, 2002).

Nevertheless, most studies on tactile suppression and modulation have focused on upper-limb actions in seated or static postures (e.g., Williams et al., 1998; Broda et al., 2020; Fuehrer et al., 2022). It remains largely unknown how tactile modulation unfolds during whole-body behaviour like postural control, where the sensorimotor system has many more inputs to handle and degrees of freedom to control. This gap limits our understanding of sensorimotor coordination in complex whole-body movements and hinders the development of models that generalize across body regions.

1.2 Predictive models and internal model theories

Efficient sensorimotor control relies not only on reactive processing of sensory inputs, but on the brain's ability to predict the consequences of its own actions. Internal model theories propose that forward models generate predictions about future sensory states based on motor commands, allowing the system to compare expected and actual input to reduce redundancy and optimize control (Blakemore et al., 1999; Wolpert & Ghahramani, 2000). In the tactile domain, this process manifests as predictive attenuation, whereby expected tactile feedback is down-weighted in perception, thereby freeing up processing resources for unexpected or externally generated stimuli (Bays & Wolpert, 1993; Kilteni & Ehrsson, 2022).

However, the conditions under which tactile input is attenuated or preserved remain complex and context dependent. While tactile suppression is commonly observed during self-initiated upper limb movements, it can also occur during passive motion (Arikan et al., 2024; Chapman & Beauchamp, 2006) or even in the absence of overt movement (Voss et al., 2006), suggesting that *motor-independent* predictions and motor-task relevance modulate these effects. Another contributing factor to suppression is tactile masking, where a stimulus is less perceived in the temporal proximity (±100 ms) of another stimulus (Abramsky et al., 1971; Kirman, 1984), which might explain suppression during passive movements (Williams & Chapman, 2002; Chapman & Beauchamp, 2006). Bayesian models of perception offer a useful framework to describe tactile suppression: sensory input and internal predictions are combined based on their respective reliability, allowing the system to flexibly adapt to uncertainty or changing sensorimotor demands (Körding & Wolpert, 2004).

Sensorimotor demands refer to the sensory information necessary for effective motor execution and the motor actions that shape or refine sensory input. Postural demands, which are a focus of this thesis, are a subgroup of motor demands that support either the maintenance of postural stability or intended changes of posture in space. These are mostly, but not exclusively, demands involving the lower limbs (Peterka, 2002).

In lower limb contexts, the mechanisms governing the adaptability of the sensorimotor system likely operate under additional constraints: gravity, postural stability, and ground interaction introduce continuous variability and demand rapid, adaptive reweighting of sensory inputs.

1.3 Postural control and multisensory integration

Predictive mechanisms typically require information to build a prediction on. Upright stance and locomotion require the seamless integration of multisensory information to estimate body orientation and generate appropriate motor responses. This process draws on visual, vestibular, proprioceptive, and cutaneous signals, which must be dynamically weighted depending on the reliability of each modality (Day, 2002; Peterka, 2002, 2018). For instance, when visual cues are unstable or misleading, as during surface sway or optic flow perturbations, the nervous system can reweight toward somatosensory input, such as afferents from the foot sole or lower leg (Assländer & Peterka, 2014; Kavounoudias et al., 2001). However, there are also findings suggesting an upweighting of visual information even when a visual-proprioceptive conflict is evoked via visual perturbations. This focus on the visual information implies a moving world and leads to downregulation of the proprioceptive signals that would suggest a static environment, resulting in posture adaptations fitting to the visual perturbations (Lishman & Lee, 1973; Chander et al., 2019; Engel et al., 2020).

Tactile signals from the lower limbs contribute critically to this sensory estimate. They either provide direct information about the supporting surface (Mouchnino et al., 2015; Mouchnino & Blouin, 2013) or can work even with low-intensity skin contact or light touch to stabilize posture by providing spatial reference information (Assländer et al., 2018; Goar et al., 2025; Jeka, 1997). However, these signals are not static. Postural state, body configuration, and attentional demands all influence how tactile information is processed. Importantly, the nervous system must continuously decide whether to up- or down-weight these signals—a process often described in terms of sensory reweighting or modulation.

1.4 Mechanisms in postural adjustment

Postural control relies on both predictive and reactive mechanisms to maintain stability in the face of internal or external perturbations. *Predictive mechanisms*, such as anticipatory postural adjustments (APAs), are initiated before a voluntary movement or expected disturbance. These adjustments redistribute body mass and preactivate postural muscles to minimize destabilization caused by the primary movement (Massion, 1992; Santos et al., 2010). APAs reflect the nervous system's ability to generate internal models of movement consequences, allowing for preemptive stabilization. In contrast, *reactive mechanisms* are elicited in response to perturbations and involve rapid sensorimotor feedback loops that trigger corrective movements, such as stepping, hip strategies, or ankle strategies (Horak & Nashner, 1986). Additionally, behavioral strategies like lowering the center of mass can increase stability by improving the base of support and reducing the likelihood of toppling. These mechanisms operate in parallel and are continuously shaped by task constraints, prior experience, and sensory input from visual, vestibular, and somatosensory systems (Peterka, 2002). Further, recent work shows that the predictability of perturbations plays a key role in how the nervous system weights APAs versus reactive responses. For example, when the perturbation direction is known in advance, APAs are more precise and timed earlier; when the direction is unpredictable, there is often a shift toward co-contraction of antagonist muscles in the anticipatory phase, possibly as a failsafe strategy (Piscitelli et al., 2017).

Effective postural control depends on the seamless integration of these processes to maintain an upright stance under dynamic and uncertain conditions.

1.5 Age-related changes in sensorimotor control

Healthy aging is associated with widespread changes in sensory, motor, and cognitive systems, which in turn affect the control of movement and posture. Sensory acuity declines across modalities, including proprioception, vestibular function, and tactile sensitivity (Seidler et al., 2010; Goble et al., 2009). These changes reduce the fidelity of afferent signals available for estimating body state, increasing uncertainty and reliance on compensatory strategies.

In the tactile domain, older adults often exhibit elevated detection thresholds or a decline in spatial acuity (Klever et al., 2019; Wolpe et al., 2016; Stevens & Choo, 1996; but see also Timar et al., 2023). These deficits can impair the timely detection of ground contact, perturbations, or slippage—sensory cues that are vital for maintaining balance. Moreover, age-related changes extend beyond peripheral loss: central processes involved in sensory integration, predictive control, and motor adaptation may also be affected (Laessoe & Voigt, 2008), and compensatory strategies such as increased visual dependence or delayed reweighting may emerge (Eikema et al., 2013; Kanekar & Aruin, 2014).

Collectively, these findings suggest that aging affects not only the fidelity of tactile afferents but also the mechanisms through which sensory input is weighted, gated, and integrated. This underscores the importance of characterizing tactile processing in the lower limbs, which are both critical for postural control and among the most informative sensory sources for estimating body orientation. Whereas failures in upper limb motor tasks may lead to relatively minor functional consequences, impairments in postural control—particularly prevalent with advancing age—carry substantially higher costs. Falls represent a major health risk in older adults and are associated with increased morbidity and mortality (Burns et al., 2016).

1.6 Theoretical framework and research objectives

Tactile perception is dynamically shaped by the interplay of predictive mechanisms, sensory reliability, and task relevance (Kilteni & Ehrsson, 2022; Körding & Wolpert, 2004; Voudouris & Fiehler, 2021). Internal forward models attenuate expected sensory input to prioritize novel or behaviorally salient signals (Blakemore et al., 1999; Wolpert & Ghahramani, 2000), while multisensory integration continuously reweights afferent input based on environmental and postural demands (Assländer & Peterka, 2014; Peterka, 2002). In the lower limbs, these modulations are crucial for balance, mobility, and interaction with the environment. Yet, the mechanisms that govern such modulation remain underexplored, particularly in ecologically valid, whole-body tasks.

Previous research has focused primarily on the upper extremities or artificially constrained conditions. We know that the lower limbs are equipped with the same type of touch sensors as the upper limbs in different configurations (Inglis et al., 2002; Trulsson, 2001), but have to solve vastly different motor tasks where failure imposes tremendous risks. Surprisingly little is known about how tactile processing in the lower limbs adapts to changes in postural stability, movement dynamics, or environmental uncertainty (Menz et al., 2006; Mouchnino et al., 2015; Mouchnino & Blouin, 2013). This is especially true in real-world contexts involving unstable support surfaces, temporally unpredictable perturbations, or object-related interactions such as foot contact. Furthermore, the extent to which these modulatory processes remain flexible in older adults, despite age-related changes in sensory and motor systems, remains poorly understood, even though their risk profile greatly increases (Burns et al., 2016).

At the core of this thesis are three primary questions. (1) How does healthy aging affect the flexibility and efficiency of tactile reweighting in balance-relevant contexts? (2) How is tactile perception in the lower limbs modulated during quasi-static tasks with varying postural demands? (3) To what extent is tactile modulation in the lower limbs shaped by sensorimotor demands, both spatially (across limbs) and temporally (across task phases)?

These questions are examined through three experimental articles, each employing vibrotactile stimulation and psychophysical threshold measurements in progressively more complex task contexts. Article 1 investigates age-related and postural influences on tactile perception during quiet stance. Article 2 explores temporal changes in tactile perception during externally induced balance perturbations in virtual reality. Article 3 examines dynamic, phase-specific tactile modulation during a goal-directed foot movement—ball kicking—focusing on interlimb differences and contact-related masking.

Together, these studies provide a multidimensional perspective on how tactile processing in the lower limbs is flexibly and efficiently regulated under varying sensorimotor demands and across the lifespan.

2 Article 1: Postural demands modulate tactile perception in the lower limb in young and older adults

(**Fabian D. Wachsmann**, Katja Fiehler, Dimitris Voudouris, *Scientific Reports*)

The first article examined how postural demands affect tactile perception in young (18–35 years) and older adults (55–75 years). Participants completed a vibrotactile detection task at the calf while either sitting, standing on solid ground, or standing on foam to manipulate postural stability. Detection thresholds served as proxies for tactile perception, and center of pressure data quantified postural sway.

As expected, postural sway was greater when standing on foam, confirming increased instability (Figure 1a). Tactile thresholds were higher under unstable conditions, indicating reduced perception. Older adults showed generally elevated thresholds, but the degree of task-dependent modulation was similar across age groups (see Figure 1b).

The findings support the notion that tactile processing in the lower limbs is adaptively modulated depending on postural context. When instability increases, the nervous system may downregulate tactile input either to minimize interference from unreliable afferent signals or as a result of masking. Although aging affects baseline perception and balance control, the preserved ability to modulate tactile input suggests that compensatory mechanisms remain effective.

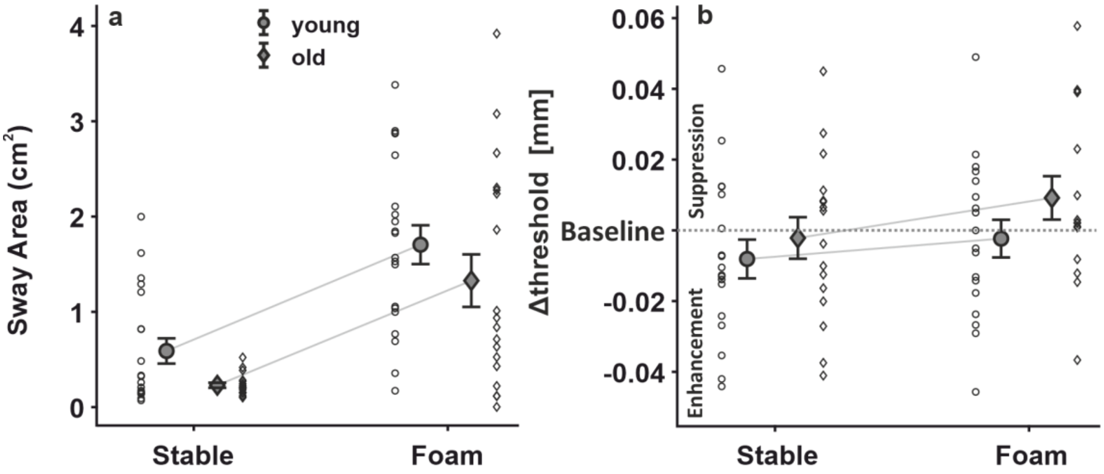

Figure 1: Effects of age and postural demands on postural sway and tactile perception. *Comparison between postural demands and age groups for (a) center of pressure sway and (b) normalized detection thresholds. Means and single subject data for young (circles) and older (diamonds) are depicted with standard errors as error bars. The horizontal dotted line in (b) represents values at baseline (sitting).*

3 Article 2: Temporal modulation of tactile perception during balance control

(**Fabian D. Wachsmann**, Katja Fiehler, Dimitris Voudouris, *Scientific Reports*)

In our second article, we examined the temporal dynamics of tactile perception during balance control and whether this modulation depends on the predictability of perturbations. Previous upper limb studies have shown that suppression is not uniform and perception can increase when tactile input becomes relevant for action (Voudouris & Fiehler, 2021). We investigated whether similar mechanisms apply to lower limbs during whole-body postural tasks.

Participants stood in an immersive virtual room while visual perturbations (forward wall motion) were presented either predictably (low uncertainty) or unpredictably (high uncertainty). Vibrotactile stimuli were delivered to the right calf at three time points: early (well before motion onset), late (shortly before), and after perturbation onset (see Figure 2). We hypothesized enhanced perception with temporal proximity to the perturbation, reflecting anticipatory gain control when tactile input becomes critical for postural adjustments.

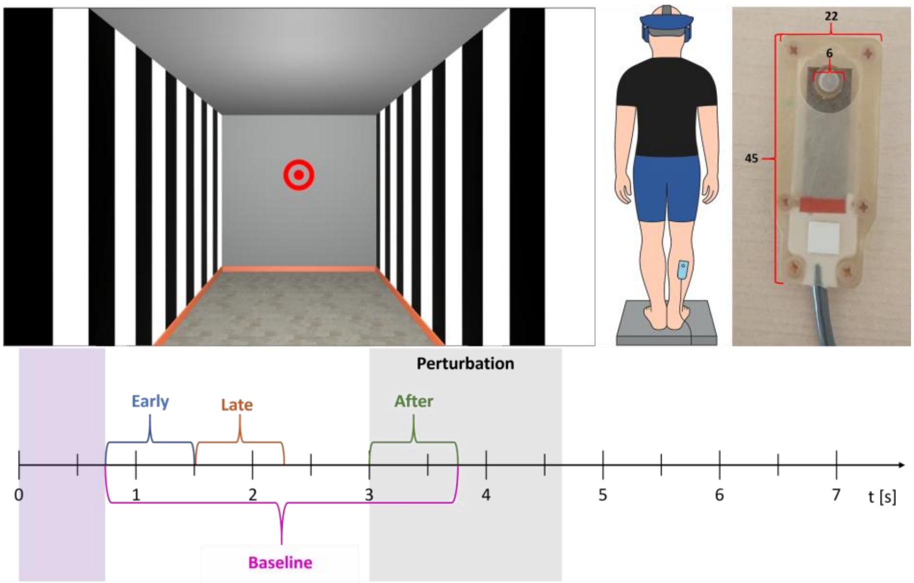

Figure 2: Experimental setup for Article 2. *Depiction of the virtual environment from the participant's view, an illustration of the setup, and a picture of the tactor. The lower panel shows a timeline of a single trial of the perturbation condition. The probe tactile stimulus in the perturbation blocks was presented at an "early" (blue), "late" (brown), or "after" (green) timepoint, whereas in the baseline condition, it could be presented at any moment during a single interval (purple). The onset of the visual perturbation is depicted as starting at the 3rd second of the trial, but this could vary in the condition with high uncertainty. The duration of the perturbation is indicated by the grey area.*

A second experiment introduced a sitting baseline to test whether the absence of suppression, as seen in movement-related upper-limb tasks, may be explained by the effects of standing per se.

Kinetic data revealed anticipatory postural adjustments in the low-uncertainty condition only (Figure 3a), without corresponding differences in tactile perception across uncertainty levels. Instead, a general increase in perception was observed after perturbation onset, indicating temporal upregulation of tactile processing approaching sensory conflict (Figure 3b). Experiment 2 replicated this temporal modulation and confirmed that standing reduces tactile perception compared to sitting.

Overall, the findings demonstrate a rapid, context-sensitive increase in tactile perception during balance destabilization. This illustrates the role of the lower-limb tactile system in supporting postural recovery via phase-specific gain control.

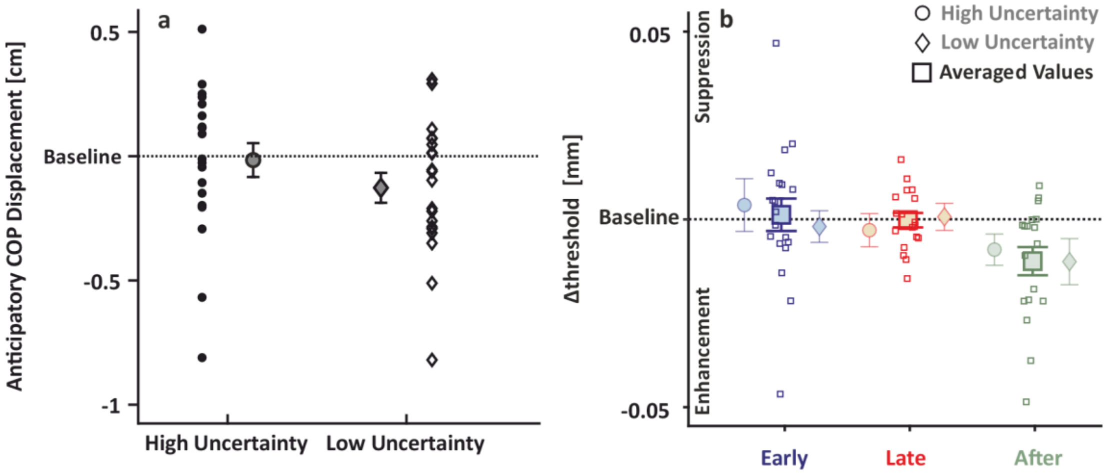

Figure 3: Results from the first experiment of Article 2. *(a) Anticipatory center of pressure (COP) displacement in the high (circle) and low (diamond) uncertainty conditions normalized to baseline. (b) Normalized detection thresholds for the same conditions, as well as the average of the two conditions (squares) for the three stimulation intervals. Means and single subject data are depicted with standard errors as error bars. The horizontal dotted lines represent values at baseline.*

4 Article 3: Modulation of tactile sensitivity in the lower limbs during goal-directed movements

(**Fabian D. Wachsmann**, Katja Fiehler, Dimitris Voudouris, *BioRxiv*)

In our third article, we investigated how tactile sensitivity is modulated across the two feet during complex goal-directed lower-limb action (ball-kicking) in which each leg fulfills a distinct functional role. We hypothesized reduced sensitivity in the balancing (left) foot during the transition to unipedal stance, due to increased postural demands, and enhanced sensitivity in the kicking (right) foot during movement phases where somatosensory feedback may guide foot trajectory. Additionally, we expected strong suppression at ball contact on the kicking foot, due to peripheral masking.

In Experiment 1, participants kicked a suspended foam ball with their right foot while receiving brief vibrotactile stimuli at four time points: movement onset, mid-swing, ball contact, and post-contact (Figure 4). Stimulation occurred either on the balancing or kicking foot. Baseline thresholds were assessed during sitting.

To isolate masking effects, Experiment 2 tested a different group of participants who remained stationary while the ball contacted their right foot at high or low speed. Vibrotactile probes were delivered at time points corresponding to mid-swing, contact, and post-contact in Experiment 1.

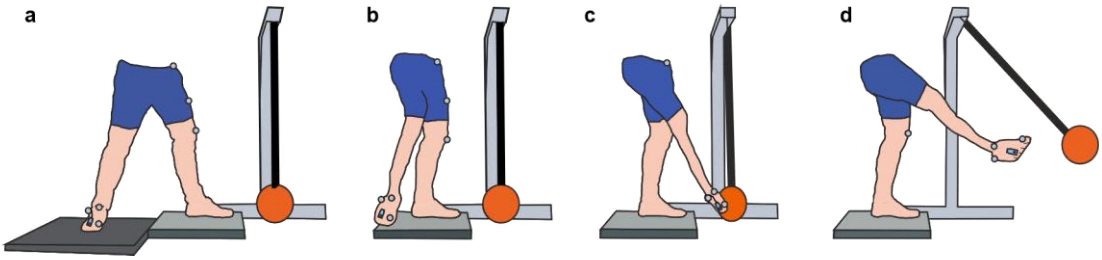

Figure 4: Kicking setup. *Sketch of the starting position, mid-swing, ball contact, and after-contact time points. Dots indicate the marker for motion tracking, and a blue rectangle the tactor position (a-d).*

This study allowed us to disentangle central sensorimotor modulation from masking effects and demonstrated that tactile sensitivity in the lower limbs is concurrently modulated across both feet, shaped by their functional role and movement phase.

Tactile sensitivity was modulated differently across the two feet. In the balancing foot, suppression peaked during the swing phase, indicating reduced processing during stance transition. In the kicking foot, sensitivity was enhanced mid-swing but dropped significantly at the moment of ball contact (Figure 5a). The degree of suppression at contact correlated with kicking velocity. In Experiment 2, we explored this correlation and showed that passive collisions with faster balls led to stronger suppression, confirming a role of peripheral masking but only at a limited window at contact (Figure 5b).

These findings demonstrate that tactile sensitivity in the lower limbs is dynamically and asymmetrically modulated during kicking actions. The balancing foot shows suppression consistent with postural transition costs, while the kicking foot exhibits a phase-dependent modulation reflecting both central (predictive) and peripheral (masking) influences. The upregulation during mid-swing suggests that somatosensory input is selectively maintained when needed for guiding in goal-directed movements. Together, these results highlight the concurrent, context-sensitive modulation of tactile information across limbs to meet the sensorimotor demands of complex actions.

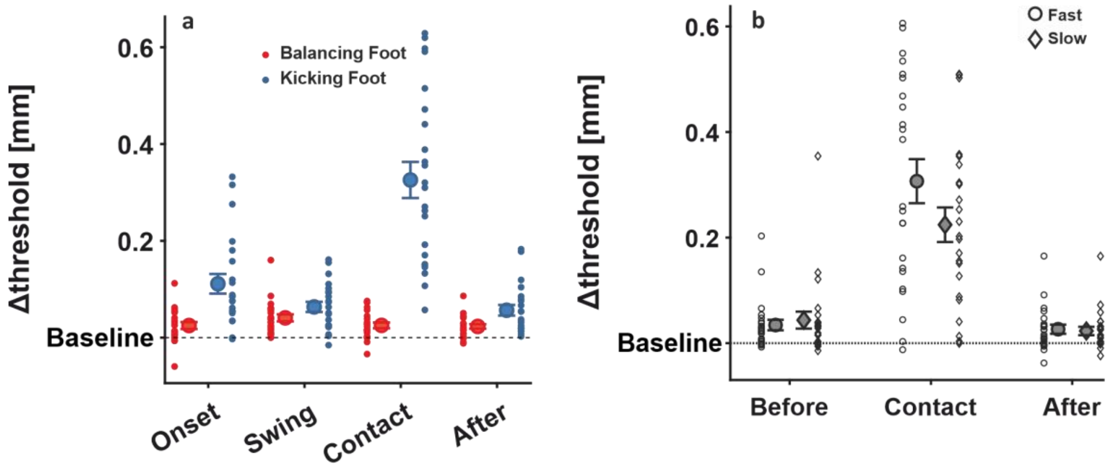

Figure 5: Limb- and phase-specific tactile modulation during kicking and ball contact. *(a) Normalized detection thresholds for all four kicking phases for Experiment 1, with data from the balancing (red) and the kicking (blue) foot. (b) Comparison between fast (circle) and slow (diamonds) contact velocities for the three probed time intervals (before, at, and after contact) of Experiment 2.* Means and single subject data are depicted with standard errors as error bars. The horizontal dotted lines represent values at baseline.

5 Discussion

5.1 Summary

This thesis investigated how tactile perception in the lower limbs is modulated by sensorimotor demands across postural and motor contexts. Three experimental articles examined modulation during upright stance, reactive and anticipatory balance adjustments, and dynamic whole-body movements.

Article 1 established that tactile perception is not constant even under seemingly stable conditions, but adapts flexibly to postural demands. When standing on unstable surfaces, tactile thresholds increased, indicating reduced perception. Although older adults exhibited generally higher thresholds, the degree of modulation was comparable to younger participants, suggesting that adaptive reweighting remains effective despite age-related sensory decline.

Building on this, Article 2 addressed the temporal dynamics of tactile modulation in the face of environmental instability. Using visual perturbations in virtual reality, it demonstrated that tactile perception increased around the onset of balance-threatening events, independent of their predictability. In contrast to the findings in the quasi-static task of Article 1, this study highlighted that tactile gain is upregulated at critical phases when sensory feedback becomes essential for postural recovery.

Article 3 extended these insights into a dynamic, goal-directed action, requiring the coordinated involvement of both legs. During a ball-kicking task, tactile perception was modulated in a phase- and limb-specific manner: the balancing foot showed suppression during unipedal stance transitions, while the kicking foot exhibited facilitation during swing and suppression at ball contact. A follow-up experiment confirmed that suppression at contact was driven by peripheral masking, revealing how central and peripheral mechanisms jointly shape tactile processing under dynamic conditions.

Taken together, the three *articles* form a progressive research arc, illustrating how tactile processing in the lower limbs is dynamically tuned to meet functional demands. This trajectory underscores the context-sensitive and multi-layered nature of somatosensory modulation in support of balance and movement control.

5.2 The role of age in tactile perception during stance retention

Previous research has shown that balance control deteriorates with age, contributing to increased postural instability and a higher incidence of falls in older adults (Burns et al., 2016; Rubenstein, 2006). Aging is also associated with a general decline in tactile perception, reflected in elevated detection thresholds (Klever et al., 2019;

Wolpe et al., 2016) and reduced spatial acuity (Stevens & Choo, 1996). We replicated these findings, with older adults exhibiting overall reduced tactile perception compared to younger participants. This decline may be due to increased peripheral noise, potentially arising from age-related changes in skin nerve fiber density (Vega et al., 2009), reduced transduction or transmission (Decorps et al., 2014), or alterations in central sensory integration (Seidler et al., 2010).

Notably, the relative modulation of tactile perception by postural challenge was comparable between young and older adults. This suggests that the mechanisms responsible for context-dependent sensory modulation, whether peripheral suppression or central deprioritization of unreliable input, remain largely intact with age. Thus, while perception at baseline may decline, the adaptive regulation of tactile input under changing sensorimotor demands appears preserved in healthy aging. This is in line with other work showing a general decline of tactile perception with age; however, increasing task demands, for example, by adding cognitive load, did not further influence tactile detection performance in the age comparison (Klever et al., 2019). Therefore, while enhancing tactile perception in older adults may represent a viable intervention target, its effectiveness is likely constrained by age-related sensory degradation. Nonetheless, the preserved capacity for adaptive sensory reweighting suggests that compensatory mechanisms remain intact and could be leveraged through context-specific or multimodal interventions.

5.3 Modulation of tactile perception by postural demands

Unlike static rest conditions in upper limb tasks, balancing is better described as quasi-static since it requires constant postural micro-adjustments. This results in an oscillatory sway pattern (Winter, 1995), which necessarily comes with muscle activity and changes of sensory input. So, the manipulation in our first article of the ground stability could have led to different results based on the literature: On the one hand, gait initiation, which puts more force and balancing demands on the leg that remains standing increases tactile processing (Mouchnino et al., 2015) and task-relevancy of tactile information enhances processing of afferent inputs from lower limbs (Staines et al., 2000) and increases tactile perception on the upper limbs (Voudouris & Fiehler, 2021). On the other hand, the rise in muscular activity, hence motor commands, and sensory noise introduced with the unstable ground would predict tactile suppression (Blakemore et al., 1999; Peterka, 2018). Our first article demonstrated that the latter mechanisms dominated tactile perception when standing on unstable ground. Interestingly, we can now add another comparison of postural demands and their effect on tactile perception by looking at standing with feet shoulder width apart (open stance), like participants did in the first article, and participants standing with their feet closer together (closed stance), like in Experiment 2 of our second article, where the base of support is reduced, so postural stability is more threatened. In both studies, stimulation was applied to the calf; however, it is important to note that we are dealing with raw data from two distinct groups of young participants with different sample sizes (18 vs. 10), which generally makes effects more difficult to detect. Despite that, we can see, by running an independent sample t-test, that the less stable group has higher detection thresholds ($t_{26} = 3.326$, $p = 0.003$, $\eta^2 = 0.301$; Figure 6). This is perfectly in line with our findings from our first article, where higher postural demands, namely standing on foam versus standing on solid ground, lead to higher detection thresholds, like standing in a closed stance does to standing in an open stance.

Beyond behavioral thresholds, neurophysiological findings provide converging evidence that tactile processing in the lower limbs is dynamically regulated at the cortical level. Staines et al. (2000) demonstrated task-dependent modulation of somatosensory evoked potentials (SEPs) recorded over S1 in the P1 and N1 components, indicating that afferent inputs from the leg are selectively amplified when task-relevant. Similarly, Mouchnino et al. (2015) observed cortical facilitation of cutaneous afferents during the planning of gait initiation, highlighting a proactive upregulation of tactile signals before balance-challenging actions. Later work further showed that SEP amplitudes are enhanced under postural instability (Saradjian et al., 2013), suggesting that the central nervous system flexibly adjusts sensory gain depending on the reliability and behavioral relevance of cutaneous inputs. These findings support the interpretation that the postural effects observed in our data cannot be explained by peripheral masking or afferent noise alone, but reflect central cortical mechanisms of sensory gating and reweighting. The integration of our threshold data with SEP evidence therefore suggests that tactile modulation in the lower limbs emerges from a close interaction between peripheral signal reliability and cortical control processes in sensorimotor networks.

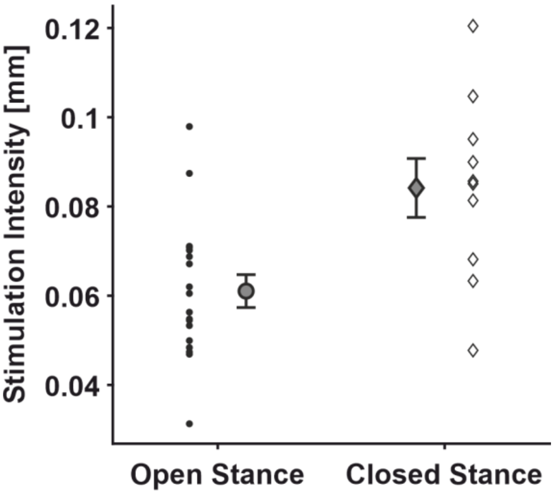

Figure 6: Reduced base of support decreases tactile perception. Comparison of tactile perception thresholds in standing on solid ground between open (circle; article 1) and closed (diamonds; article 2) stance. Means and single subject data are depicted with standard errors as error bars.

5.4 Sensorimotor demands and tactile modulation

In addition to postural demands, we manipulated external visual input by introducing temporally uncertain optic flow (article 2), and we varied movement demands by probing tactile perception in both legs across different time points (article 3).

It is well established that visual perturbations challenge postural control, eliciting both anticipatory and reactive adjustments (Chander et al., 2019; Lee & Lishman, 1975; Lishman & Lee, 1973). Optic flow stimuli have even been shown to induce congruent center of pressure sway patterns both in real-world moving rooms (Lishman & Lee, 1973; Lee & Lishman, 1975) and in virtual reality (Chander et al., 2019; Engel et al., 2020; Phillips et al., 2022). In our second article, we replicated these findings, particularly the anticipatory postural adjustments when perturbation timing was predictable.

What remained unknown, however, was how the tactile system responds to such visually induced instability. One might expect that postural responses, especially when postural adjustments follow the direction of the visual perturbation, would be the result of a relative increase in reliance on vision and a relative reduction in reliance on non-visual input, such as tactile signals. Additionally, high predictability of object properties can reduce tactile perception compared to low predictability in grasping (Voudouris et al., 2019). Our results revealed the opposite pattern: tactile perception increased in response to visual perturbations, regardless of whether their onset was predictable or not. This suggests that instability in the external environment elevates the *need* for reliable multisensory information, thereby *upregulating* tactile perception. In other words, rather than being suppressed under visual dominance, tactile perception was enhanced under dynamic, balance-threatening conditions. This is in line with research showing increases in cortical excitability during haptic exploration compared to just movement, since the need for tactile information increases (Oliver & Tremblay, 2009), the increase in phases of high guiding demands (Voudouris & Fiehler, 2021), the additional information needed when initiating a step (Mouchnino et al., 2015), or the finding that adding sensory demands for movement execution, increases processing in the moving lower limb (Staines et al., 2000). It also supports models of dynamic sensory reweighting under postural challenge, where cutaneous input is enhanced when other channels (e.g., vision or proprioception) become unreliable (Peterka, 2002; Assländer & Peterka, 2014).

The temporally precise changes observed in our second article, modulated by environmental instability, were already remarkable. In our third article, we extended this approach by examining the temporal modulation of intentional movement, focusing on two functionally distinct legs during a naturalistic kicking task.

The balancing leg had to stabilize the body while transitioning from bipedal to unipedal stance. Based on our previous findings, we expected tactile perception to be impaired during this high-postural-demand phase and to recover afterward. The kicking leg, in contrast, was engaged in a goal-directed movement. Drawing on analogies to upper-limb actions, we hypothesized a facilitation of tactile perception during the swing phase, when guiding demands increase (Voudouris & Fiehler, 2021).

Critically, these opposite modulations were expected to occur within the same movement phase, the swing phase, and this is precisely what we observed. This finding demonstrates that tactile processing is not only finely tuned in accordance with sensorimotor demands during movement, but also operates independently for different limbs based on their functional role. This replicates a pattern of perceptual modulation on the static and active upper limb while reaching to one's own hand (Voudouris & Fiehler, 2017, 2021). This work is the first to show independent modulation on different limbs in the presence of differing and complex motor tasks. It further supports the idea of an efficient, demand-driven sensory system, potentially shaped by constraints in central processing capacity or the general tendency for optimization (Wolpert & Ghahramani, 2000).

We also examined how external noise, such as ball contact, interferes with tactile perception. Our results showed that suppression at the moment of contact was not merely the result of predictive attenuation based on expected sensory consequences but also occurred when the timing of contact was unknown. We interpret this as tactile masking: the suppression scaled with the intensity of the masking stimulus and was temporally confined to a narrow window around the moment of contact, with rapid recovery shortly thereafter, in line with typical descriptions (Abramsky et al., 1971; Kirman, 1984). While we replicated that masking stimulus intensity plays a significant role, there are further findings like the specificity of masking effect to certain mechanoreceptors (Gescheider et al., 1989) or the effect of masking stimulus duration (Gescheider et al., 1995). These are unlikely to affect our results of the masking study where the ball contact was short, constant in duration, and of no specific frequency; however, the movement in a balancing task, such as rapid adjustments, is of longer duration and might cause more intense or longer masking effects.

It remains unclear whether this suppression reflects a purposeful mechanism to discard unreliable input or whether it results from the sheer intensity of stimulation overwhelming the system's capacity to transduce, transmit, or process tactile information. In either case, the findings highlight once more the fast adaptability of the human tactile system.

6 Conclusion

Like the gymnast introduced at the beginning of this synopsis, the sensorimotor system must constantly recalibrate its stance in response to shifting internal goals and external conditions. The findings of this dissertation highlight that tactile perception in the lower limbs is neither globally suppressed nor passively received, but flexibly modulated based on the postural, temporal, and functional demands of the task. Perception decreases when afferent input is less reliable or less behaviorally relevant and increases when tactile cues support task execution—be it standing, responding to perturbations, or executing dynamic foot movements.

Rather than representing a fixed suppression mechanism, tactile modulation appears to follow a context-sensitive logic. Across all three experimental articles, tactile thresholds were shaped by whether a limb was engaged in stabilization, movement initiation, or interaction with external objects. This dynamic tuning reflects the integration of predictive models and sensory feedback, whereby afferent signals are weighted based on their reliability and task relevance.

Taken together, these results support an embodied model of sensorimotor control in which tactile input is continuously evaluated and reweighted to facilitate adaptive behavior. The lower limbs, often overlooked in tactile research, emerge here as critical sensory sources—not only for estimating body orientation but for guiding anticipatory and reactive adjustments under changing demands.

Beyond its theoretical contribution, this work may inform interventions to support postural stability in populations at elevated fall risk. As tactile reweighting remains intact in older adults despite sensory decline, context-specific augmentation—such as vibrotactile feedback, adaptive footwear, or balance training—may improve stability not by boosting perception at baseline, but by enhancing conditions that prioritize critical input. Understanding how and when the system modulates lower-limb input offers a foundation for assistive technologies that align with the adaptive logic of sensory integration.

In returning to the gymnast metaphor, the nervous system, much like the athlete, continuously reconfigures its stance in response to both internal goals and external instability. Tactile perception in the lower limbs thus plays a pivotal role in maintaining this fine balance – one that is continuously renegotiated to keep us standing tall and moving forward.

7 References

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II. Publications

1 Publication 1

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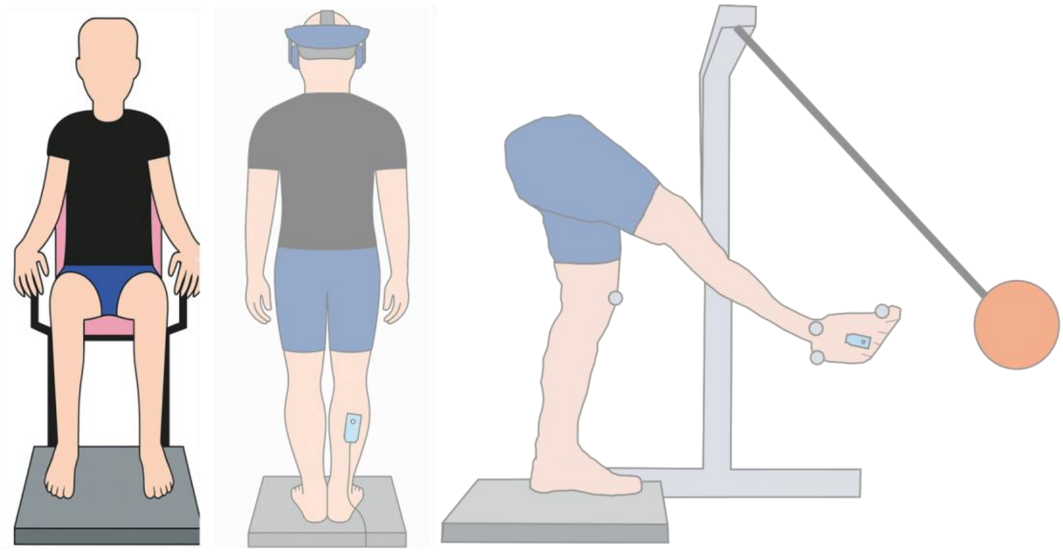

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Postural demands modulate tactile perception in the lower limb in young and older adults

Fabian Dominik Wachsmann✉, **Katja Fiehler** & **Dimitris Voudouris**

Balance control requires the continuous integration of feedback signals from several sensory organs with feedforward estimates about the state of the body. Such feedback signals are important for standing upright, as shown in increased and more variable sway patterns when sensory feedback is compromised, for instance when standing with eyes closed or on unstable surfaces that make cutaneous signals from the foot less reliable. Poorer sensory processing is also considered to arise during healthy aging due to a decrease of the reliability and transmission rate of feedback signals. Here, we are interested in how processing of tactile signals from the lower leg is modulated when balance control is challenged and how this interacts with age-related sensorimotor changes. We examined tactile sensitivity on the lower leg during sitting, standing on stable ground, and standing on unstable ground (foam). We quantified the center of pressure during the two standing conditions by determining the area of a 95% confidence interval ellipse as well as the total displacement of the center of pressure. Tactile sensitivity was assessed by asking participants to detect brief vibrotactile probes of various intensities to the lower leg. As expected, postural sway increased when standing on foam than stable ground for both age groups. When postural demands were minimal (sitting), tactile sensitivity was overall poorer in older than younger adults. Tactile perception was also poorer when standing on foam than on the stable ground, for both age groups. We conclude that increased postural demands reduce reliance on tactile signals from the lower limb in both young and older adults.

Keywords Balance control, Posture, Tactile modulation, Aging

Standing upright requires a sophisticated interplay between feedback and feedforward processes. Humans estimate the current state of their body stance by sampling and synthesizing visual, vestibular, proprioceptive, and tactile signals based on their reliability[1,2] and integrate this sensory information with previous experiences about the prevailing dynamics to generate descending motor commands and efference copies, through which they can establish sensorimotor predictions about future sensory states[3]. This process requires access to the most recent sensory input, which can facilitate postural adjustments to retain upright stance.

Poorer sensory input can lead to compromised postural control[2]. For example, when people stand with eyes closed, their centre of pressure (COP) can be subject to larger and more variable displacements[4] indicating postural instability. Besides vision, somatosensation plays a central role in keeping upright. For example, lightly touching an object with the upper-limb can reduce postural sway, even when the contact forces do not offer sufficient physical support[5,6]. Such light touch provides tactile and proprioceptive signals about arm position, which can inform the postural system about necessary adjustments, and even reduce the impact of hampered sensory input from other modalities that might have a destabilizing effect on posture[7]. In addition to light touch, cutaneous signals from the lower limb have a key role in postural control. Obviously, cutaneous afferents from the foot sole provide key information about the state of the upright body[8] so when cutaneous input from the foot sole is degraded, such as when standing on surfaces of low compliance (e.g., foam), postural sway increases[9–11]. Although the foot sole is the primary somatosensory access point to obtain information about the relationship between the standing body and the ground, cutaneous signals also from other parts of their lower limb can contribute to postural control. For example, light pressure arising at the lower leg can reduce postural sway, and the contribution of these input signals is even more pronounced when they arise further away from the foot (e.g., at the knee and calf compared to the ankle;[12]). Moreover, cutaneous afferents from the lower leg encode information about the direction of ankle movements, and this information matches well the directional

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information conveyed by the lower leg muscles[13]. This further highlights the central role of tactile feedback signals from the lower leg to estimate the sensory state of the limb, and to control whole-body posture.

Despite the importance of tactile signals for movement control, tactile sensitivity is often compromised in a limb that is about to move or is already in motion. Voluntary movements can suppress tactile signals arising from the moving limb, a phenomenon known as *tactile suppression*. This suppression primarily stems from central efference copy mechanisms[14,15] which predict the sensory states of the moving limb and downweigh associated feedback. However, peripheral processes related to movement, such as proprioceptive afferents generated by the action itself, may also suppress tactile stimuli on the moving limb, likely through masking. For instance, suppression is evident also during passive movements[16–18] where the involvement of descending motor commands is unlikely. Importantly, tactile suppression is not an all-or-nothing mechanism but is modulated by task demands. For example, suppression weakens, disappears, or even reverses to tactile enhancement when somatosensory feedback from the probed limb is critical for the task. As a matter of fact, the strength of tactile suppression during sensory-guided reaching or grasping is temporally modulated, as suppression can diminish at critical moments[19,20]. Similarly, while standing, tactile sensitivity from the lower leg increases shortly before a visual perturbation that could destabilize balance[21]. Interestingly, tactile afferents from a stationary leg can also be enhanced shortly before the other leg initiates a step, as the stimulated leg becomes important for supporting whole-body balance[22]. Additionally, afferents from the ankle joint are enhanced just before the stimulated leg touches the ground during locomotion[23]. Together, these findings suggest that afferent signals from various body parts are processed dynamically, depending on their relevance to the task at hand.

Sensory processing is typically poorer in healthy aging[24,25] while sensorimotor functions are slower as humans grow older[25,26]. Such compromised sensorimotor processes may explain why some studies demonstrate stronger reliance on predictive control during aging. Accordingly, tactile suppression increases in older adults[24,27],but see also[28] which might reflect a compensatory mechanism to adapt to the poorer sensorimotor functionality. However, other studies show poorer predictive control in older than younger adults, as reflected in smaller and delayed anticipatory postural adjustments before self-imposed perturbations[29]. So far, it is unknown how processing of tactile information from the lower leg, which is essential for maintaining upright balance, is modulated by postural demands and their associated motor responses in healthy young and older adults.

Here, we examined the modulation of tactile signals from the lower leg when participants were either sitting, standing on stable ground, or standing on an unstable (foam) surface. We expected increased postural sway when standing on an unstable than stable surface in both age groups. Based on previous work[24,25] we further expected poorer tactile sensitivity at the lower leg during sitting, when no postural demands are introduced, in older compared to younger adults. If standing on an unstable surface requires increased reliance on feedback signals from the lower leg, tactile sensitivity on the lower leg might be enhanced when standing on foam than on stable ground. Alternatively, if standing on an unstable surface introduces increased afferent inflow due to muscle stiffness or pronounced sway, tactile suppression might be stronger when standing on foam than on stable ground. If aging influences tactile suppression depending on the postural demands, there should be an interaction.

Methods

Participants

We recruited 23 young (24.04 ± 4.25 years old, range: 18–35; height: 171.26 ± 10.72 cm; 17♀, 6♂) and 20 older (64.10 ± 5.09 years old, range: 55–72; height: 170.15 ± 10.76 cm; 15♀, 5♂) healthy participants. They were free from any known neurological or musculoskeletal issues at the moment of the experiment that could hinder their participation, and they had normal or corrected-to-normal vision. Younger participants were recruited from student pools of the Justus Liebig University Giessen. Older participants were community-dwelling and were recruited through personal contacts of the authors and through internal mailing lists of the Justus Liebig University Giessen. All participants or their legal guardians signed an informed consent. The study was approved by the local ethics committee of the Justus Liebig University Giessen. All methods were carried out in accordance with the "World Medical Association Declaration of Helsinki" (2013, except for § 35, pre-registration)[30]. At the end of the experiment, participants received either 8€/hour or course credits.

Apparatus

A custom-made vibrotactile stimulation device (Engineer Acoustics Inc., Florida, US), which will be referred to as a "tactor", was attached to the skin over the *musculus gastrocnemius lateralis* of the participant's right calf, a muscle primarily used for balance control[31]. This tactor consists of a small housing (22 × 45 × 5 mm) and a round actuator (6 mm in diameter) that can generate vibrotactile stimuli of fine-grained duration, frequency and amplitude. The tactor was fixed at 3 cm medial of 2/3 of an imaginary line connecting the heel with the *caput fibulae*. The tactile device was securely positioned in that specific spot and delivered probe tactile stimuli of various intensities that act as a proxy for tactile processing during upright stance. This particular body part was chosen based on previous studies showing that tactile input from the lower leg plays a crucial role in postural control[12,21]. Unlike the foot sole or Achilles' tendon, this area experiences minimal skin deformation, which is a known confounding factor in tactile perception[32]. Additional tape was used to fix loose wires or clothing to the participant's body so that they would not cause sensations that could be misinterpreted as vibrations or interfere with task performance. To manipulate the postural demands and their associated motor responses, we asked participants to either sit, stand on a stable surface, or stand on a piece of foam, similarly to previous work[11,33]. We used a force plate (AccuSway, AMTI, Massachusetts, US) to sample the (COP) at 300 Hz to assess postural behaviour in the two standing conditions only. In the sitting condition, participants sat on a chair with their feet on the force plate and their knees at ~90 deg. In the standing condition, they stood directly on the force plate

(∼5 cm from the ground), while in the foam condition participants stood on a balance pad (50 × 40 × 6 cm, density of 81.3 kg/m^3; SISSEL BalanceFit Pad, novacare GmbH, Bad Dürkheim, Germany) that was placed on top of the force plate. Participants had their feet at shoulder-width apart in all three conditions. They could also choose to be either barefoot or with their socks on, and were required to retain this choice throughout the experiment. To ensure a comfortable and safe environment, an additional experimenter stood beside the participant to reduce any possible fear of falling by providing support in the unlikely event of a fall (no participant ever fell). For the standing conditions, participants were upright with their arms relaxed at their sides and had to fixate a circular point (18 cm diameter) on the facing wall, ~ 230 cm in front of them and at a height of 185 cm.

Procedure

Data acquisition as well as pre-processing and analysis were handled by custom-made Matlab R2021a software (The Mathworks, Massachusetts, US).

The experiment consisted of 5 phases (familiarization, training, and three experimental blocks). During familiarization, we presented 5 trials with a vibrotactile probe (50 ms, 250 Hz) to the participant's lower leg while standing, ranging from low (peak-to-peak amplitude: 31.6 µm) to strong (peak-to-peak amplitude: 284.4 µm) intensities. This familiarization phase allowed participants to understand how the stimuli felt. Please note that this vibration is irrelevant for movement control and is used as a proxy to probe tactile perception on a body part that is relevant for the performed task, similarly to the procedure used to probe tactile suppression during arm and finger movements e.g.[14,34]. In addition, the intensity and duration of those probe vibrations are much different from those known to cause illusory postural sensations through the activation of Golgi tendon organs and muscle spindles e.g.[35,36].

A training phase that included 10 trials was presented after the familiarization procedure. Participants now stood on the force plate. Each trial started with the experimenter pressing a button that triggered data collection and within a variable interval of 2–3 s after that moment, a vibrotactile probing stimulus (50 ms, 250 Hz) of various intensities was presented at their lower leg. An auditory cue indicated the end of the trial right after the vibration and prompted participants to respond as to whether they had noticed a tactile stimulus, if they had not responded already. An experimenter logged the responses to the host PC via button presses. The stimulus intensity for each trial was determined using a QUEST algorithm (Psychtoolbox Version 3.0.18), which employs a Bayesian approach to estimate psychometric function parameters using prior knowledge. We used a Weibull function with $\beta = 3.5$, as recommended for two-alternative forced choice tasks[37] while the prior mean and standard deviation were estimated from a pilot study with young participants standing with their feet together ($N = 16$; exposed to 50 stimuli of varying intensities). We conducted the training phase to ensure participants fully understood the task and could accurately identify the relevant tactile probes. This step was crucial, as the quality of initial trials in a QUEST staircase method directly influences the determination of the intensities of subsequent trials.

This training phase was followed by the 3 experimental blocks, each consisting of a single condition (sitting, stable, foam; Fig. 1), presented in random order. Each experimental block was preceded by a calibration phase consisting of 20 trials, during which the intensities of the tactile probes were recalibrated using a QUEST algorithm with parameters identical to those previously described. The reason for doing so was not only the fact that individual detection thresholds are considerably variable across participants e.g.[38] and differ between age-groups e.g.[24], but that they may also differ under various postural demands. Therefore, we aimed to determine a suitable probing intensity range for each participant and for the underlying postural condition. Once these 20 trials were completed, we used the mean of the estimated probability density function to construct a range of probing stimuli for the respective participant and postural condition. This allowed us to tailor our probing stimulus range around each participant's detection threshold and therefore to minimize the risk of ceiling or floor effects. We used this range of stimuli to assess tactile perception with the method of constant stimuli during the experimental blocks. The range was constructed by choosing 6 stimulus intensities that were weaker and another 6 intensities that were stronger than the threshold estimated by the QUEST, resulting in a total of 13 intensities (including the QUEST threshold) that were separated by a peak-to-peak displacement of the actuator equal to 6.32 µm. Sometimes the estimated QUEST threshold was so low that it was not feasible to choose 6 unique intensities below the QUEST threshold that were both positive and non-zero. In such cases (17 blocks in 11 participants) every intensity level that would correspond to an intensity of 0 or lower was handled as a level without stimulation (catch trial). The resulting range of presented stimuli can therefore be different for every condition and participant to optimize psychometric probing and fitting. We presented 6 trials for each stimulus level that had an intensity larger than 0, and another 22 mandatory catch (no-stimulation) trials resulting in a total of 100 trials per postural condition. The intensities of the probing stimuli were presented in a random order within each block. While participants were allowed to take breaks and sit at a chair next to the force plate whenever they wanted, mandatory breaks of at least one minute were enforced during both standing conditions after 20 QUEST trials and after every 25th trial. As in the training phase, the tactile probe was presented within 2–3 s after trial onset and, again, the end of a trial was indicated by an auditory cue.

Each trial lasted ~ 5 s, including the time window for responding to the tactile stimulus. This might appear short for assessing postural behavior, as most studies examine body balance in longer time intervals (e.g., 30 s). However, our main interest is in assessing tactile sensitivity, which requires several trials. In our experiment we presented more than 300 trials per participant, and so we decided to keep the duration of each trial short to facilitate the experimental procedure, especially for our older adults.

Data analysis

To evaluate whether upright stance changed between the two standing conditions, we analyzed COP characteristics. We first pre-processed the COP data by subtracting the mean mediolateral and anteroposterior

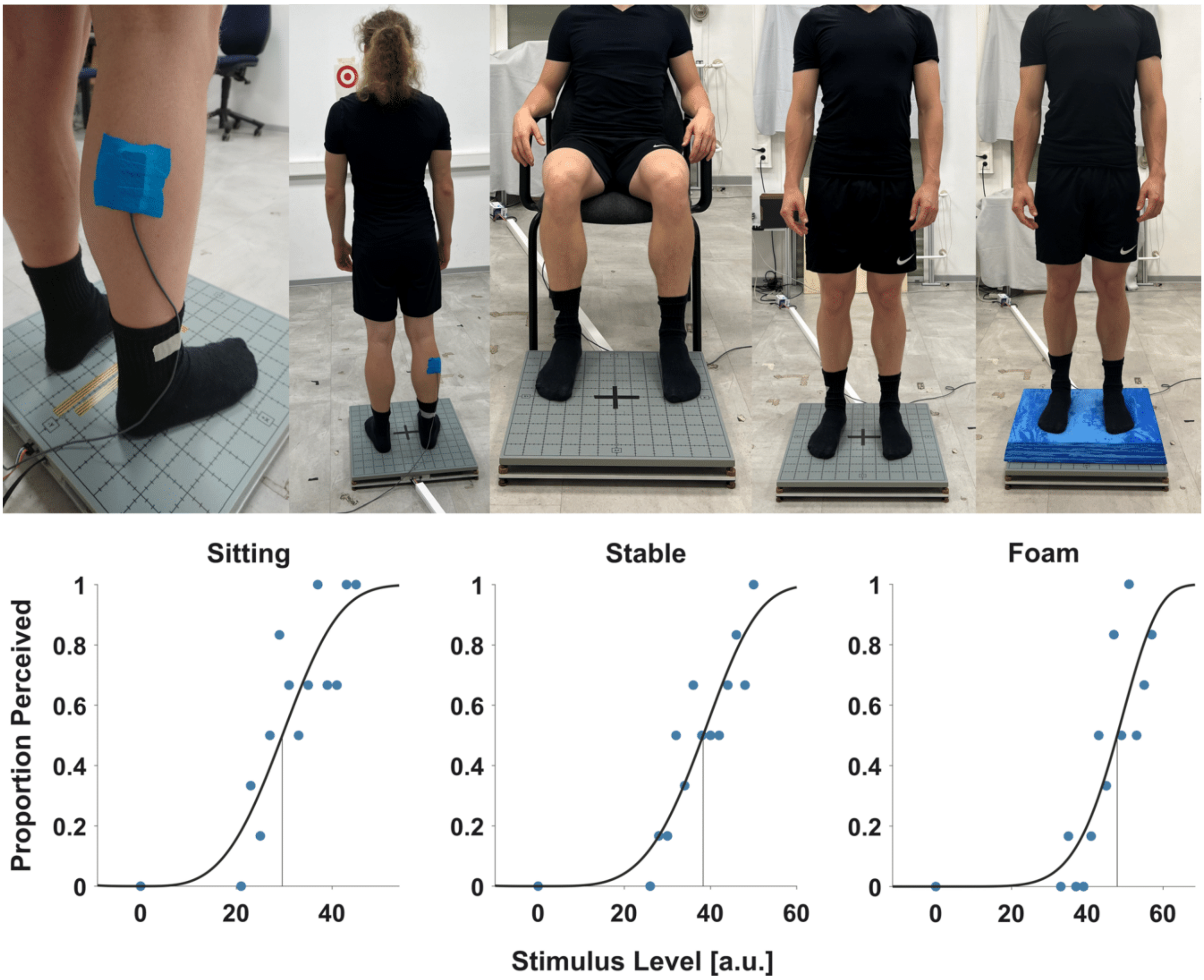

Fig. 1. **Experimental setup and psychometric functions.** From left to right in the upper panel, pictures of the tactor placement, the fixation location (red circle), the sitting, the stable standing, and the unstable standing condition. In the lower panel there are 3 exemplary psychometric functions for the three conditions from the first participant. Blue dots represent the ratio with which stimuli of different intensities were perceived. The units are arbitrary. The vertical line indicates the estimated detection threshold as the 50% level.

values from each trial's time-series data. We then smoothed the data using a zero-lag, 4th-order Butterworth low-pass filter with a 10 Hz cutoff. Since the tactile probe was presented at the earliest within 2 s after trial onset, which was critical to keep the duration of the experiment within reasonable limits, we truncated our COP data to include the samples obtained during the first 2 s of each trial, eventually excluding any possible influence of the tactile stimulation itself and of the verbal response to this tactile stimulus on posture (see Fig. 2). It is, however, important to note that participants stood on the force plate for the whole block of 100 trials and the first trial started after a brief familiarization phase, so any non-stationary parts that appear in the beginning of standing task are reduced[39]. For each trial we calculated the area of a 95% confidence interval ellipse of the COP data, further called *sway area*, to quantify stability in the spatial domain. We also calculated the total two-dimensional displacement of the COP path, further called *sway length*, to quantify stability more in the temporal domain. We then averaged these values across all trials per condition of each participant.

To evaluate how perception of tactile signals is influenced by the underlying postural conditions and for each age group, we fitted the responses to tactile stimuli in each of the three postural conditions, separately for each participant, with a Weibull function using the Psignifit 4 toolbox[40] in Matlab. We defined the tactile detection threshold as the stimulus intensity at a 50% detection rate, adjusting for lapse and guess rates. The slope at this threshold served as a measure of perceptual sensitivity. To assess tactile modulation during standing while also accounting for individual differences in tactile perception during rest (sitting baseline), we normalized each participant's detection thresholds and slopes by subtracting their sitting baseline values from those obtained in the two standing conditions, resulting in two normalized threshold and slope values per participant (Δthreshold and Δslope).

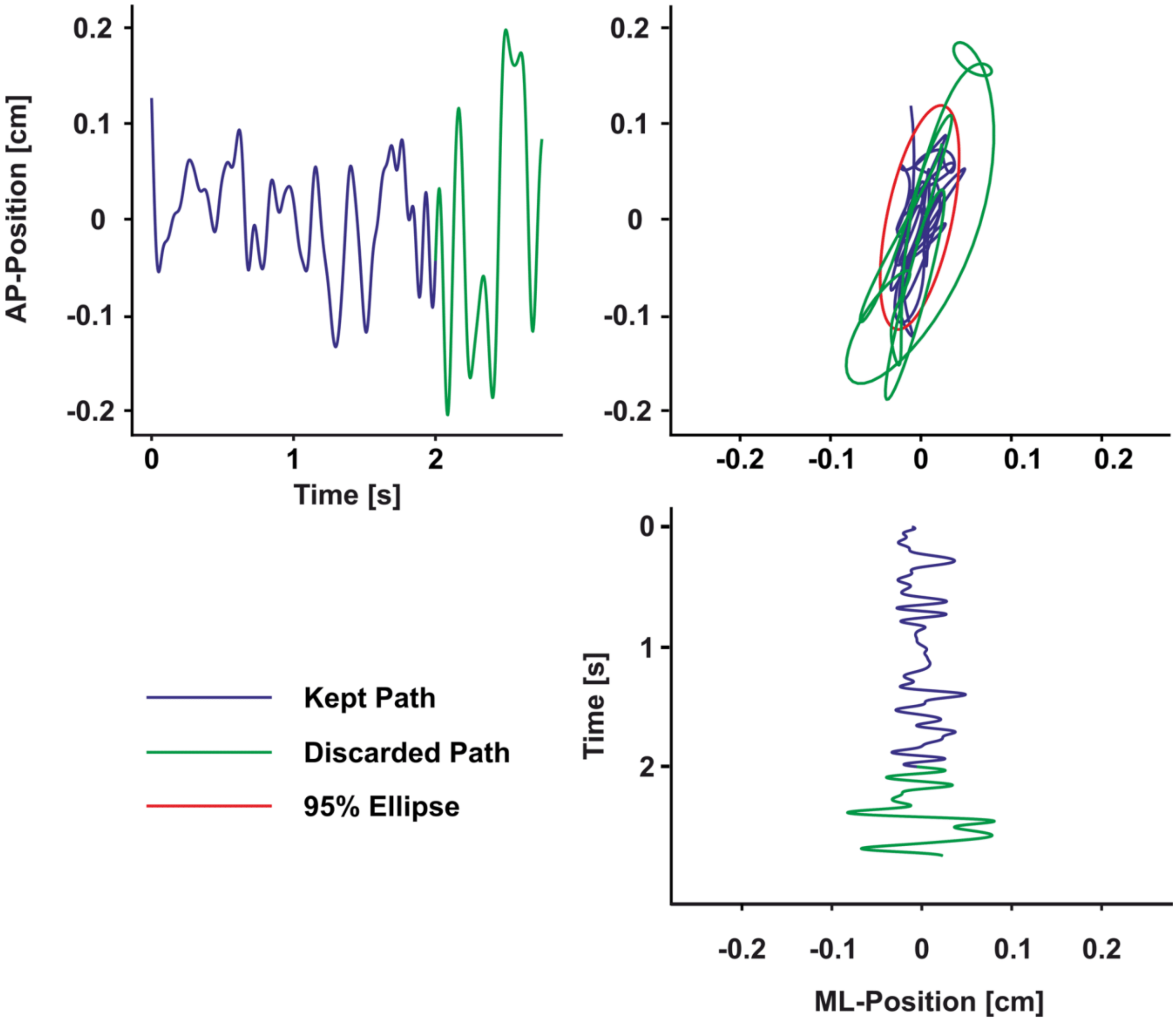

Fig. 2. **Kinetic data preparation.** The panels show the statokinesiogram of the anterior-posterior position (top-left) and the medio-lateral position (bottom-right) of the center of pressure within one trial. On the top-right is the stabilogram of that same trial. Blue lines indicate the 2 s truncated data that went into the analysis, while the green lines are the discarded rest of the trial. The red ellipse corresponds to the sway area analysis.

Three young participants were excluded from all kinetic analyses due to a technical malfunction of the force plate, leaving us with a sample of 20 younger and 20 older adults with full data sets. We were first interested in whether tactile sensitivity changes as a function of age. We decided to focus on tactile sensitivity only during sitting as this provided us with pure age-related sensory changes in tactile sensitivity, taking out any possible influences of posture itself. For instance, when standing, there may be differences in skin stretch or muscle activity at the lower leg, which can influence on their own tactile sensitivity[32]. In addition, performing a tactile detection task while maintaining balance or not could impair the simultaneously performed perceptual task[41] which could have influenced tactile sensitivity across participants and age groups.

For the analysis, we first confirmed that the false alarm rates during the sitting baseline were smaller than 0.2. In a second step, we excluded participants from the baseline analysis if their estimated baseline thresholds were beyond the strongest intensity presented in that block (1 younger and 2 older adults). Consequently, these three participants were also excluded from the Δthreshold and Δslope analyses because these two analyses require reliable sitting baseline values. In addition, participants with a false alarm rate above 0.2 or estimated thresholds beyond the stimulation range in at least one standing condition were excluded from the Δthreshold and Δslope analyses (3 young, 1 old). In a final step, we excluded participants as outliers if their datapoints were outside of a 2 interquartile range. This was done separately for the baseline and the Δthreshold/Δslope analyses. It resulted in additionally excluding 2 young adults from the baseline thresholds, 2 young and 2 old adults for the baseline slopes, 1 young and 1 old adult for the Δthresholds, and 4 young and 7 old adults for the Δslopes.

For the kinetics, we excluded participants as outliers based on the interquartile ranges of each of the two variables. Specifically, we excluded only 2 old participants based on their sway area and another 2 old participants based on their sway length values. No young adult was excluded from the kinetic analyses.

Statistical analysis

To examine if postural demands affect upright stance in young and older adults, we conducted two separate 2 (age groups) x 2 (postural demands) repeated measures mixed ANOVAs on sway area and sway length (38 datasets). To confirm that aging reduces overall tactile perception, as has been shown before[25] we compared detection thresholds (38 datasets) and slopes (36 datasets) during the sitting baseline between age groups using one-sided independent t-tests. To examine the modulation of tactile sensitivity as a function of postural demands and aging, we conducted two separate 2 × 2 repeated measures mixed ANOVAs with the factor's postural demands (stable, foam) and age (young, old) on the normalized detection thresholds (34 datasets) and slopes (26 datasets). We set our alpha to 0.05, and we report effect sizes as η_{part}^2 following the calculations and recommendations by Corell[42]. Statistical analyses were conducted in JASP version 0.18.1 (University of Amsterdam, The Netherlands).

Results

Kinetics

As expected, sway area and sway length were higher when standing on foam than on the stable surface (area: $F_{1,36} = 47.492$, $p < 0.001$, $\eta_{part}^2 = 0.569$; length: $F_{1,63} = 54.624$, $p < 0.001$, $\eta_{part}^2 = 0.603$; Fig. 3a-b), confirming that our experimental manipulation led to the expected increase in postural sway. However, sway area did not differ between age groups ($F_{1,36} = 3.274$, $p = 0.079$, $\eta_{part}^2 = 0.083$) and there was no interaction ($F_{1,36} = 0.003$, $p = 0.956$, $\eta_{part}^2 < 0.001$). Sway length was also not influenced by aging ($F_{1,36} = 0.128$, $p = 0.723$, $\eta_{part}^2 = 0.004$) and there was no interaction either ($F_{1,36} = 0.741$, $p = 0.395$, $\eta_{part}^2 = 0.020$).

Tactile perception

Older adults had overall higher detection thresholds than young adults during sitting ($t_{36} = 1.843$, $p = 0.037$, $\eta^2 = 0.082$; Fig. 4a), in line with previous findings showing poorer tactile sensitivity in aging[24]. However, there were no statistically significant differences in the slopes of the baseline psychometric functions between the two age groups ($t_{34} = 0.482$, $p = 0.683$, $\eta_{part}^2 = 0.007$; Fig. 4b).

After establishing that standing on foam influences posture and that aging reduces tactile sensitivity, we sought to examine how standing on stable and unstable surfaces influences tactile processing from the lower limbs in our two age groups. Tactile thresholds were higher when standing on foam than on the stable surface ($F_{1,32} = 13.284$, $p < 0.001$, $\eta_{part}^2 = 0.293$). However, there was neither a main effect of age ($F_{1,32} = 1.282$, $p = 0.266$, $\eta_{part}^2 = 0.039$), nor an interaction ($F_{1,32} = 1.414$, $p = 0.243$, $\eta_{part}^2 = 0.042$; Fig. 5a). There were also no main effects or an interaction for the slopes ($F_{1,24} <= 2.508$, $p >= 0.126$, $\eta_{part}^2 <= 0.095$; Fig. 5b).

Discussion

We examined whether perception of tactile signals from the lower limb is modulated by postural demands and during healthy aging. We confirm previous results e.g.[43,44], showing that standing on a surface of low

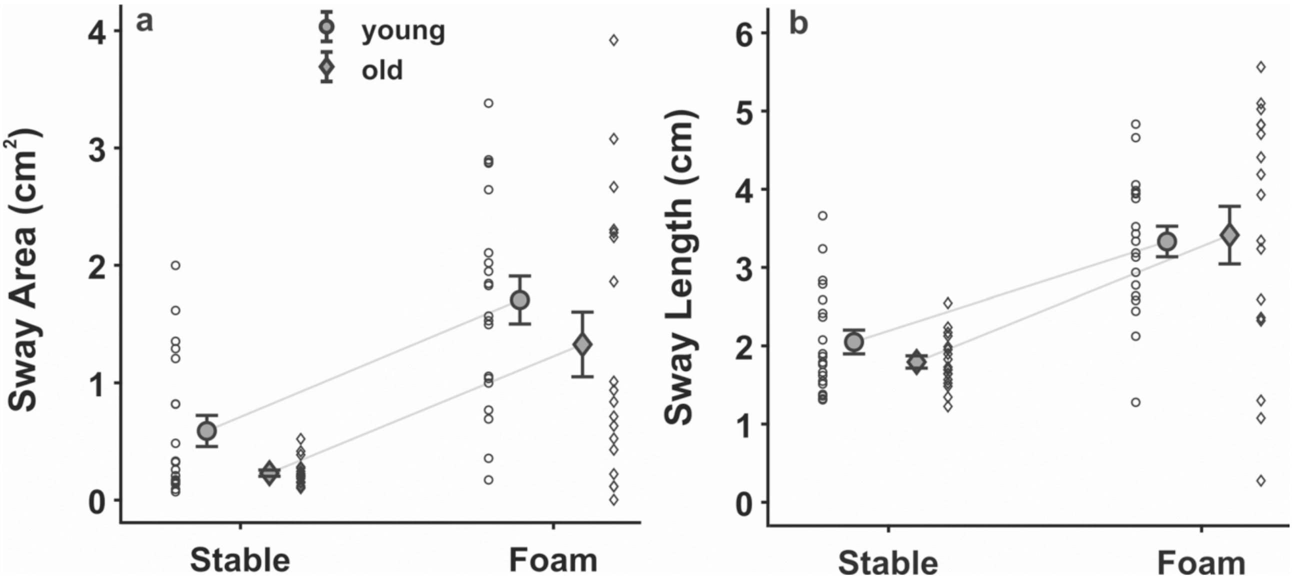

Fig. 3. **Kinetic modulation.** Comparison between postural demands and age group for (**a**) sway area, as indicated by the 95% Confidence Interval of the COP, and (**b**) sway length, as indicated by the total length of the COP. Means and single subject data for the young (circles) and older adults (diamonds) are depicted with standard error as error bars.

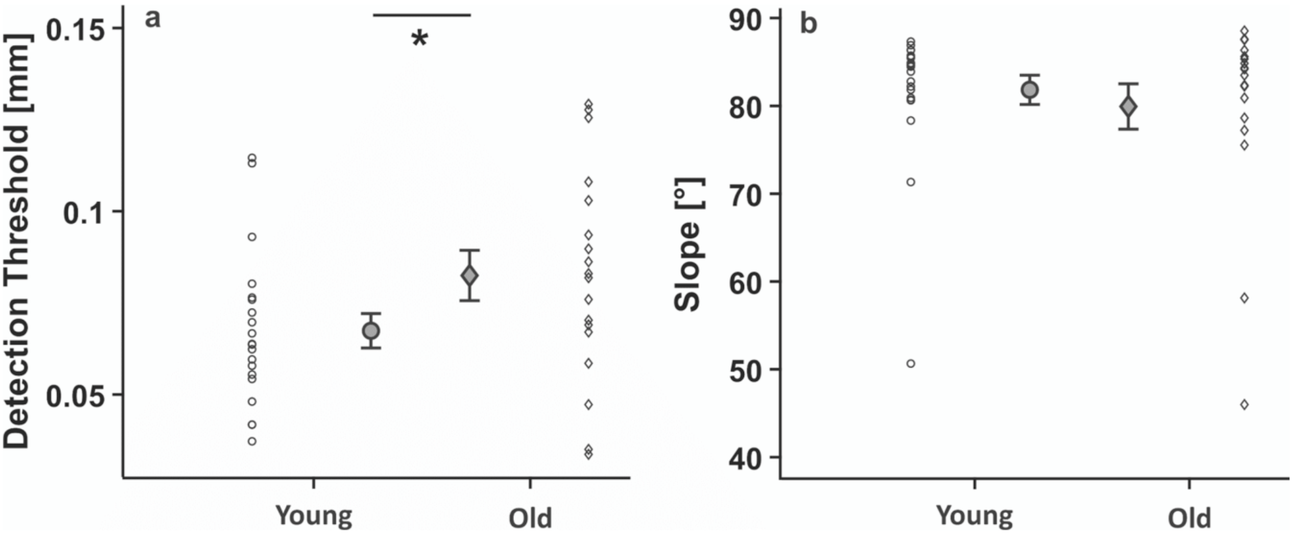

Fig. 4. **Age effects on tactile perception during sitting.** Comparison between the age groups for (**a**) detection thresholds, and (**b**) slope of the psychometric function in the baseline, sitting condition. Means and single subject data for the young (circles) and older adults (diamonds) are depicted with standard error as error bars. * $p < 0.05$.

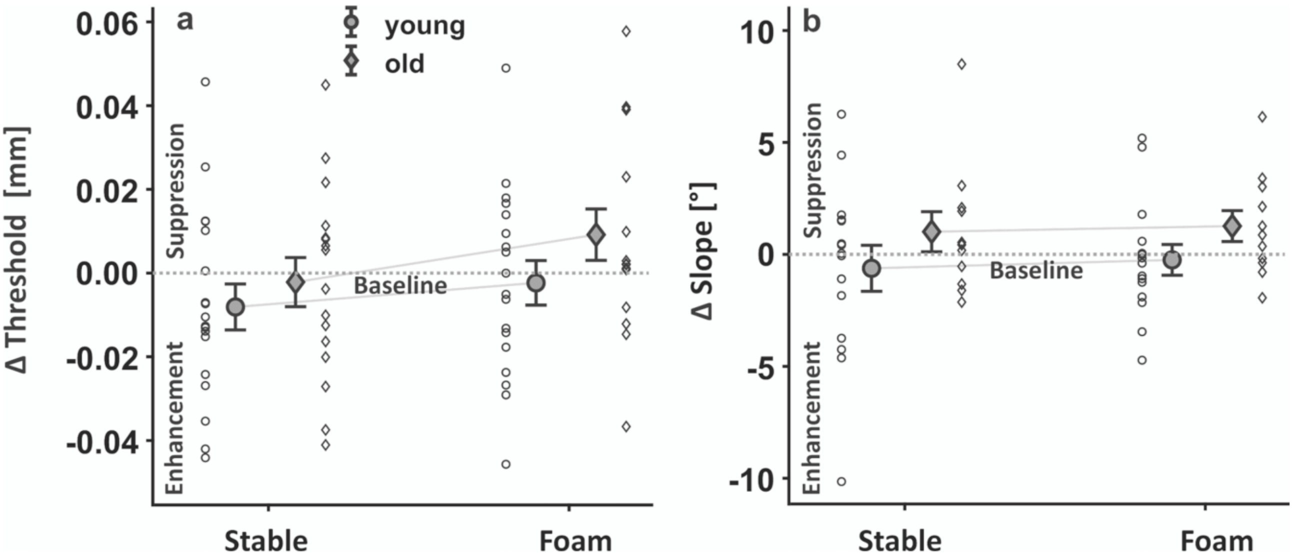

Fig. 5. **Effects of age and postural demands on tactile modulation.** Comparison between postural demands and age group for (**a**) normalized detection thresholds, and (**b**) normalized slopes. Means and single subject data for the young (circles) and older adults (diamonds) are depicted with standard error as error bars. Horizontal dotted lines represent values at sitting (baseline).

compliance (foam) increases postural demands as reflected in pronounced postural sway. As expected[24,25], we found poorer tactile sensitivity during sitting in older than in young adults. Our main finding is that tactile perception decreased with higher postural demands, and this decrease did not differ between the two age groups. Specifically, tactile sensitivity was poorer when standing on an unstable surface than on a stable surface in both young and older adults.

It may seem paradoxical that tactile sensitivity decreased when postural demands increased, because reduced tactile sensitivity from the lower limb may impede feedback processing that is relevant for the task at hand. Our results are in line with previous work showing poorer tactile perception when standing on a narrow base of support compared to sitting[21]. However, they are at odds with previous reports demonstrating improved tactile sensitivity on a limb that is involved in a task that requires pronounced sensory guidance during movement execution[34,45], and around postural transitions[22,23]. Why did our participants perceive and incorporate less tactile information when their upright posture was challenged? One possible explanation comes from recent findings showing an increase in tactile suppression with an increase in global task load[4647]. However, this possibility would not explain the above-mentioned results e.g.[22,45], which found *weaker* tactile suppression or even tactile enhancement when task demands increase. A reduction in tactile perception when standing on foam than on a stable surface might indicate a shift in prioritization of posture at the expense of the simultaneously performed perceptual task e.g.[41]. However, the slopes of the psychometric functions did not differ between conditions, indicating similar performance in the discrimination of adjacent stimulus levels. Moreover, no changes in false alarm rates were observed across conditions or age groups, showing that response biases did not change. These two factors would suggest no change in prioritization; however, they cannot rule out this possibility entirely.

Another possibility that would explain the decreased sensitivity when standing on foam is that afferent signals from the leg, such as those arising from increased muscular activity to maintain upright stance, were stronger when standing on foam than on the stable surface. For instance, increased muscle activity or larger sway movements when standing on foam might have masked the tactile probe that we used to assess tactile sensitivity. Previous studies show that afferent signals can backward mask brief tactile probes presented around one's own movement, and that such masking can partly explain tactile suppression[17]. This explanation also aligns with our previous study showing poorer tactile sensitivity when standing with a narrow base of support on a firm surface, which required increased muscular activations to maintain upright stance in a virtual reality setting[21]. However, in the current study we did not find tactile suppression when standing on the firm surface relative to sitting (modulation around zero in Fig. 5a; old: both $t <= 1.796$, both $p >= 0.091$, both $\eta^2 <= 0.045$, young: both $t <= 1.689$, both $p >= 0.109$, both $\eta^2 <= 0.036$). This might be due to some methodological differences, such as the vision of a virtual world environment versus real world, or differences in postural configuration. For instance, standing with the feet closed together, as done in the previous study[21], limits the base of support and likely requires stronger muscle activations of the calf, compared to when standing with a wide base of support, as done in the current study. The possibility of increased muscular activations when standing on a narrow base of support might have led to pronounced masking processes that could have impaired perception of the probing stimuli in the previous study. However, considering that the influence of afferent signals on tactile masking is not systematic e.g.[16,48], we can only speculate about the precise mechanisms behind the decreased tactile sensitivity with higher postural demand.

Although aging led to higher detection thresholds during sitting, confirming that aging compromised tactile sensitivity, we did *not* find any evidence that postural demands influence tactile sensitivity differently in young and older adults. This lack of an age effect may be explained by the absence of age-related differences in sway area or path length, which could have indicated a greater need for modulation of tactile processing in older adults. The lack of an age-effect in sway area is in line with previous findings showing that postural sway does not differ between older and younger adults[49] or it may be even smaller in aging[50]. Older adults can compensate for their sensorimotor decline by increasing the co-activation of their ankle muscles[51]. In this case, one might have expected stronger masking of the probing stimulus due to the muscle stiffness, which we do not observe. Please note that we have not measured muscular activity, so this remains a hypothesis for future research. In sum, we show that tactile suppression during standing is stronger with higher postural demands in both young and older adults. These results highlight the contribution of tactile information in postural control and their dependencies on the task demands irrespective of age.

Limitations

The presented work is primarily limited by two factors. First, our cohort of older adults is relatively young, given that we included participants above the age of 55 years. However, as sensory decline is a gradual process, a 40-year difference between the two groups, as evident in our samples, enables us to examine how sensorimotor processes, such as tactile sensitivity and postural control, are reflected in the aging sensorimotor system. The observed effects may become even more pronounced with increasing age, as sensory and motor processes are further declined[26].

The second limitation pertains to the relatively short trial durations employed in the kinetic analysis. Although this duration allows for the assessment of changes in postural control, it limits the accurate quantification of lower-frequency sway components (below 0.5 Hz), which are known to contribute substantially to overall postural sway[52]. Precise estimation of these frequencies would require longer trial durations. However, this was not feasible in our psychophysical study with the primary focus on sensory modulations, which necessitates a high number of trials for reliable sensory threshold quantification. Nonetheless, we were able to demonstrate kinetic changes associated with postural demands; thus, short trial durations are sufficient to capture the increased postural sway when standing on surfaces of lower compliance. The lack of an age-effect on postural behavior may come as a surprise, however, it is consistent with previous studies that did not obtain evidence for age-related differences in balance control, even when using longer trial durations[49].

Data availability

Behavioral and psychophysical data are publicly available after acceptance at https://osf.io/jwghy/. For further information or data requests please correspond to Fabian Dominik Wachsmann (Fabian.Wachsmann@psychol.uni-giessen.de).

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Author contributions

Conceptualization: F.W., K.F., D.V.Data curation: F.W.Formal analysis: F.W.Funding acquisition: K.F., D.V.Investigation: F.W.Methodology: F.W., K.F., D.V.Project administration: F.W., K.F., D.V.Resources: F.W., K.F., D.V. Software: F.W.Supervision: K.F., D.V.Validation: F.W., K.F., D.V.Visualization: F.W.Roles/Writing - original draft: F.W.and Writing - review & editing: F.W., K.F., D.V.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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2 Publication 2

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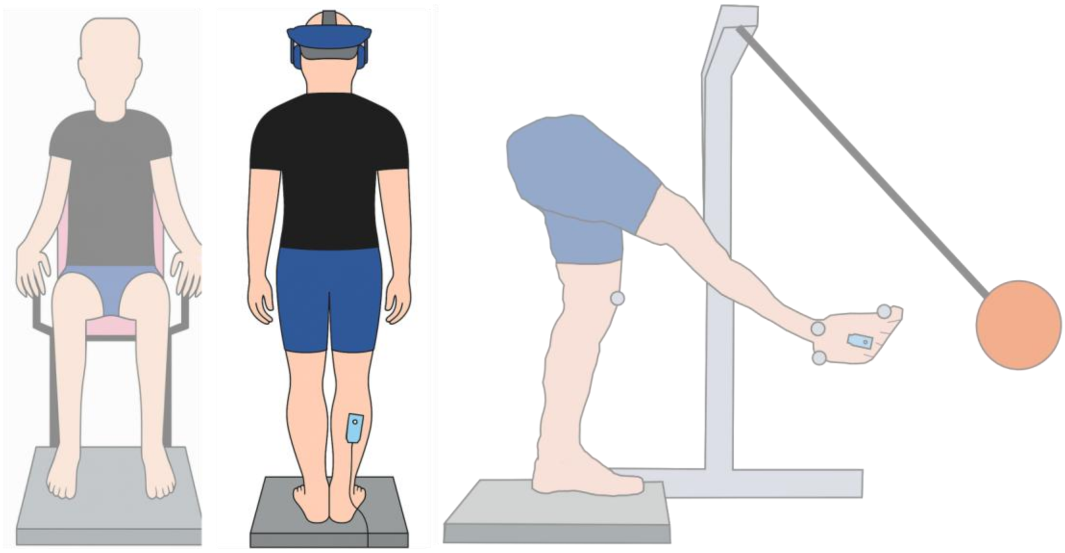

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Temporal modulation of tactile perception during balance control

Fabian Dominik Wachsmann✉, Katja Fiehler & Dimitris Voudouris

Somatosensory feedback, like touch, is essential for body control and movement. Yet tactile sensations from a body part that is about to move or is moving are often suppressed. Most studies on tactile suppression focus on upper-limb movements, where suppression is typically reduced when tactile signals become important to the task. However, how tactile sensitivity changes at other body parts involved in more complex, whole-body actions is widely unexplored. This study examines the temporal tuning of tactile processing on the lower limb during balance control while varying feedback processing demands. Participants stood in a virtual room, with the front wall moving toward them at a moment of high or low temporal uncertainty challenging their posture. Tactile sensitivity was probed using vibrotactile stimuli at the lower leg at different time points relative to perturbation onset. We found that tactile sensitivity while standing improved around the time of perturbation, irrespective of the temporal uncertainty about perturbation onset. Such dynamic modulation indicates a continuous process of sensory feedback regulation to accomplish the task at hand. This expands previous knowledge about sensory integration on the lower limbs during postural control.

Keywords Perception & action, Postural adjustments, Tactile modulation, Virtual reality

Tactile sensitivity on a moving limb compared to the same limb in a static state is reduced. This is typically reflected in poorer sensitivity to externally-generated probe tactile stimuli that are delivered to a limb while being engaged in movement planning or execution. This tactile suppression is shown in simple finger extensions, and more complex upper-limb actions such as reaching, grasping and even juggling[1–5], with reduced tactile sensitivity observed at both perceptual[1,4,5]and neural levels[6–8]. Although tactile suppression can be partly explained by peripheral mechanisms, such as additional reafferent signals masking the probe tactile stimuli[2,9], see also[10], the prevailing idea is that sensorimotor predictions down-weight the incoming sensory feedback arising from the movement[11,12].

Tactile suppression of vibrotactile probes on a moving limb can be modulated by various factors. For instance, when the sensations arising on a moving limb are highly predictable, tactile suppression on that limb increases[2,13]. On the other hand, tactile suppression is reduced on a moving limb when sensory feedback from that limb is needed to accomplish the task. For instance, tactile suppression on the index finger of a grasping hand is reduced when grasping objects of unknown properties or of low friction[14,15], reflecting that the increased need to sample tactile information for accomplishing the motor task allows the sensorimotor system to tune tactile suppression of afferent signals. The tuning of tactile sensitivity on a moving limb is also reflected in dynamic temporal changes during the execution of arm movements[16–18]. Indeed, tactile suppression is reduced at moments of the reaching phase when sensory guidance of the arm's movement gains importance[18]. All in all, these results reflect that tactile sensitivity on a body part largely depends on the dynamic interplay between central predictive and somatosensory feedback signals.

Despite the large body of research on the modulation of tactile processing, mechanisms underlying up- and down-regulation of tactile signals during whole body movements are still unclear. For instance, some studies found that somatosensory-evoked potentials (SSEPs) related to tactile stimulation on the foot sole are decreased prior to a foot flexion[e.g.19]. However, other studies revealed an opposite pattern with increased SSEPs prior to step initiation[20]. This apparent discrepancy in physiological signal processing may arise from the different needs to use tactile feedback for the actions in question, as has been proposed for upper limb movements. Specifically, prior to initiating a step[20], tactile sensitivity on the foot sole may improve as tactile feedback from that body part provides crucial information for balance control. In contrast, tactile feedback from the foot sole prior to an arbitrary foot flexion[19] may be less relevant for movement execution and thus it may be down-regulated. The modulation of tactile sensitivity during postural control is not surprising as it is observed in various instances and across various sensory modalities. For instance, H- and T-reflexes are inhibited when postural demands increase[21,22], presumably as a protective mechanism that facilitates balance. In addition, vestibular signals are

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suppressed when artificial delays are introduced between the generation of ankle torques when standing and the consequent whole-body responses[23]. However, when participants are exposed for long enough to learn the coupling between the generation of the torques and the delayed sensorimotor consequences, vestibular signal integration recovers[23]. Another example for vestibular reweighting can be observed during postural transitions from standing to locomotion with a reduction of vestibular signal processing during the transition phase[24]. Modulation of other sensory signals, such as proprioceptive signals, can also be observed when anticipating the avoidance of a virtual ball. Visual signals are up-weighted while proprioceptive signals from the lower leg are down-weighted, though this modulation can be reversed with more exposure to the task[25]. Considering that processing of sensory signals related to upright stance is modulated by the task dynamics, we are here interested in examining how tactile processing is tuned when confronted with various postural demands. Specifically, we test the hypothesis that tactile sensitivity is modulated by the need to process tactile feedback from the lower leg that is involved in the retention of upright posture. We applied a common psychophysical approach allowing us to compare our results to previous work on tactile suppression during upper limb movements[13,26].

Tactile information is important for maintaining upright posture. For instance, tactile signals from the foot sole, including plantar cutaneous afferents, convey spatiotemporal information about skin stretch and pressure variations[27,28], and these signals can be used to adjust body posture accordingly. Tactile signals from the foot sole are also integrated prior to the initiation of an upcoming step[29], whereas disrupting the quality of tactile information from the foot sole can result in poorer upright stance[30,31]. However, tactile information from other body parts can also play an important role for maintaining upright stance. A common instance refers to tactile signals that arise when lightly touching a surface with the finger or hand, which can facilitate postural sway, even when touch force levels do not physically support the body[32,33]. This light touch could provide somatosensory (i.e., tactile and proprioceptive) signals about arm position, which could inform the postural system about necessary adjustments, and even down-weight the contribution of other sensory inputs, such as electrical vestibular stimulation, which could disturb balance[34]. However, light-touch is not the only touch-related input that can influence balance control, as passively obtained tactile information can also facilitate posture. Specifically, rubbing a piece of fabric at the skin over the shoulder area can lead to reduced postural sway in young, older and pathological populations[35]. Similar results have been found when rubbing tactile stimuli (e.g., Velcro materials) at various positions of the lower leg, such as between the knee and the ankle. In sum, several studies have shown that tactile signals from various body parts, including the lower legs, can provide crucial information to support body balance[36] and to obtain a better estimate of the current body configuration to facilitate postural adjustments. Based on these, if tactile processing is modulated at moments when somatosensory control of posture gains importance, we expect improved tactile sensitivity on the lower leg at moments when tactile input can be useful for postural control, such as before the onset of a postural adjustment in response to a perturbation.

To examine how tactile sensitivity on the lower leg is modulated by postural demands that can impact feedback processing for balance control, we asked participants to stand within a virtual room, facing a wall that would move towards them with low or high temporal uncertainty. This visual perturbation was introduced to challenge balance control, as has been shown in several previous studies[37–39]. When the perturbation is of high temporal uncertainty, and thus its onset cannot be easily predicted, we expect merely reactive postural adjustments. In contrast, when the perturbation is of low temporal uncertainty, and thus its onset is well-predictable, we expect anticipatory behaviour to the perturbations, and any reactive adjustments should be smaller compared to those elicited in the condition with a high temporal uncertainty. Importantly, to probe tactile sensitivity, we presented a brief tactile stimulus of varying intensity to the participant's lower leg at various moments prior to and immediately after the onset of the visual perturbation, and participants had to verbally report whether they felt it or not. By presenting the probing stimuli to the skin over the calf area, instead of other areas, such as the foot sole, we not only assess how tactile input from that area is modulated by postural demands, but we also avoid confounds caused by pronounced skin deformations on the foot sole during postural sway that could themselves influence tactile perception[40]. In addition, this approach is similar to examining tactile sensitivity during upper limb movements, such as grasping actions, when the tactile probe is delivered around the area of the involved effector but not directly to the skin area engaged in the task e.g., fingertip during grasping[1,13,41]. Here, we probed the skin over the calf muscle that is in close proximity to the direct contact area between body and floor (foot sole), bearing in mind that the calf area conveys important tactile signals that can improve body posture[35,36]. It is also important to note that the probing tactile stimuli are neither informative nor relevant for maintaining upright stance in our study.

To confirm that our manipulation had the expected effects on body posture, we examined whether postural sway was reduced in anticipation of perturbations with low temporal uncertainty[25]and whether body sway increased after the onset of either type of perturbation. To examine these, we first assessed the idiosyncratic body sway in a baseline, quiet stance condition, where no perturbation was presented, and we subtracted each individual's baseline sway from that during the perturbation trials. With respect to tactile modulation, we expected altered tactile sensitivity during perturbation compared to quiet stance trials. The main purpose of our study is to examine whether postural demands change the reliance on tactile feedback processing from the lower limb, and thus whether tactile sensitivity is temporally modulated during postural control. Based on findings from goal-directed arm movements[16,18], we expected a temporal modulation reflected in increased tactile sensitivity at moments when postural demands are high, such as around the time of a postural reaction, where one needs to maintain posture in the presence of perturbation. Finally, we explored if any temporal modulation in tactile sensitivity differs between the two types of perturbations (high vs. low temporal uncertainty). In a second experiment, we explored whether the requirement to keep upright imposes any further changes in tactile sensitivity on the lower limb. To this end, we tested whether tactile sensitivity changes between standing and sitting.

Results

Participants stood in a virtual room with the instruction to fixate a circular target on the front wall. In two separate blocks of trials, they were confronted with a visual perturbation that entailed the complete room moving in a way that the front wall approached them. Each of these blocks included perturbations that were initiated with a low uncertainty (i.e. after the presentation of a countdown) or high uncertainty manner (i.e. no countdown). A vibrotactile probe was applied to the skin of the participants' calf at three possible moments during each trial: at one of 2 time windows before the onset of the perturbation, or at one time window right after the onset of the perturbation (*early*: −2.25 to −1.50 s; *late*: −1.50 to −0.75 s; *after*: 0.00 to 0.75 s; all relative to perturbation onset). Participants had to verbally respond if they felt the vibration, and we used the responses to determine detection thresholds based on an adaptive method (QUEST) applied separately per condition and participant. The following results focus on the participants' behavior assessed by the center of pressure (COP) and their head kinematics, and on tactile perception.

Experiment 1

Kinematics

As expected, anticipatory postural behavior was generally evident prior to the low uncertainty perturbation compared to the respective baseline. Specifically, the maximal displacement of the COP was smaller during the period before the expected visual perturbation than during the respective quiet stance baseline (t_{19} = 2.114, p = 0.024, η^2 = 0.053; Fig. 1a). This is in line with our hypothesis based on previous work[25]. However, the head's maximal displacement before the expected visual perturbation was not systematically different from that during baseline (t_{18} = 1.420, p = 0.086, η^2 = 0.026; Fig. 1b). Meanwhile, and as expected, there was no evidence of anticipatory behavior prior to the high uncertainty perturbation, as reflected both in the COP and the head maximal displacements (both $t < = 0.202$, both $p > = 0.842$, both $\eta^2 < = 0.001$). These findings confirm that participants considered the underlying dynamics of the perturbations and predictively tuned their posture whenever possible.

Unsurprisingly, postural sway was larger when reacting to the low uncertainty perturbation relative to quiet stance, as reflected both in the COP (t_{18} = 3.402, p = 0.002, η^2 = 0.132; Fig. 1c) and the head kinematics (t_{19} = 2.849, p = 0.005, η^2 = 0.097; Fig. 1d). Likewise, sway amplitudes were larger during the reaction to the high uncertainty perturbation relative to quiet stance, evident both in the COP (t_{19} = 3.664, $p < 0.001$, η^2 = 0.144) and the head kinematics (t_{19} = 3.261, p = 0.002, η^2 = 0.117). These results indicate kinematic compensations of the visual perturbation in both perturbation conditions.

Tactile sensitivity

We assessed tactile sensitivity by calculating tactile detection thresholds through an adaptive procedure (QUEST). Figure 2 shows the distribution of the number of trials required for the QUEST algorithm to converge to the estimated detection threshold, for each of the 173 estimations. We presented 30 trials per block, and the average number of trials to estimate the detection threshold was only 8.3 (SD: 2.3). Thus, the number of trials per block was enough to obtain a detection threshold.

Raw detection thresholds for each of the 3 time intervals during the perturbation blocks are depicted in Fig. 3a. Although some detection thresholds during the perturbation blocks appear to differ from those obtained during the respective standing baseline, on average the detection thresholds during perturbation blocks were not systematically different from those obtained during baseline (all $t < = 1.933$, all $p > = 0.069$, $\eta^2 < = 0.047$).

Tactile perception during perturbation blocks relative to the standing (quiet stance) baseline (which we hereafter refer to as *Δthreshold*) was temporally modulated as reflected in a main effect of time ($F_{2,28}$ = 4.364, p = 0.022 η^2 = 0.054; Fig. 3b). Post hoc t-tests revealed significantly lower detection thresholds in the "after" compared to the "early" interval (t_{18} = 2.942, p = 0.019, η^2 = 0.064), but there were no statistically significant differences for the thresholds between the "late" and "after" intervals (t_{18} = 1.699, p = 0.201, η^2 = 0.022), nor between the "early" and "late" intervals (t_{18} = 1.243, p = 0.224, η^2 = 0.012). These indicate that tactile sensitivity improved during the period immediately after the onset of the visual perturbation, at least relative to the "early" pre-perturbation period. There was no main effect of temporal uncertainty ($F_{1,14}$ = 0.364, p = 0.556, η^2 = 0.012) nor an interaction between uncertainty and time ($F_{2,28}$ = 0.190, p = 0.828, η^2 = 0.004).

Experiment 2

We conducted Experiment 2 to test if standing already causes an elevation of the tactile detection thresholds, which might marginalize any possible additional effects of feedback processing demands on tactile detection thresholds during the perturbation trials as was previously shown for foot sole stimulation[42]. To this end, we first contrasted tactile sensitivity during quiet stance against a new sitting baseline. Indeed, standing itself led to reduced tactile sensitivity (t_9 = 2.285, p = 0.048, η^2 = 0.115; Fig. 4), in line with previous work[42].

Raw detection thresholds during the 3 time intervals of the perturbation blocks in Experiment 2 are shown in Fig. 5a. On average these thresholds were higher than the detection thresholds obtained in the sitting baseline (all $t > = 2.213$, all $p < = 0.027$, all $\eta^2 > = 0.109$; Fig. 5b). These show a clear decline in tactile sensitivity during standing in the perturbation trials compared to sitting.

As in Experiment 1, the 3 × 2 ANOVA on Δthresholds revealed a main effect of time ($F_{2,16}$ = 16.159, $p < 0.001$, η^2 = 0.247; Fig. 5), showing that tactile sensitivity was temporally modulated while anticipating and reacting to perturbations. Specifically, tactile detection thresholds were reduced in the "after" compared to the "early" (t_8 = 5.455, $p < 0.001$, η^2 = 0.108) and "late" (t_8 = 4.113, p = 0.002, η^2 = 0.064) intervals, and did not differ between the "early" and the "late" intervals (t_8 = 1.342, p = 0.171, η^2 = 0.07). These are in line with the findings of Experiment 1 and demonstrate improved sensitivity at times around the time of perturbation, thus at moments when sensory

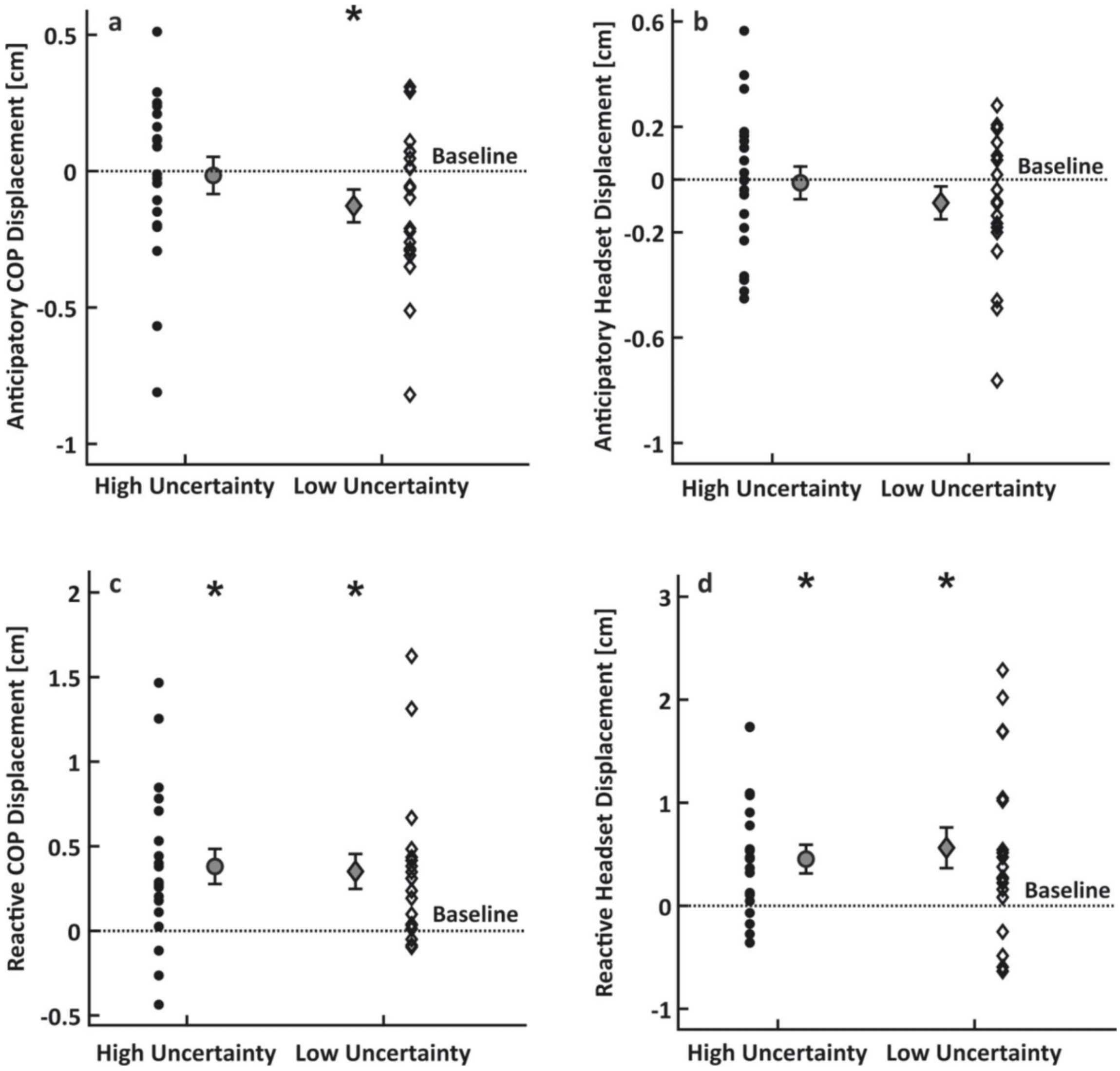

Fig. 1. Results of the kinematic analysis. COP and head kinematic results for the anticipation and reaction periods. Panels a and b show anticipatory COP and head kinematic behavior, respectively. Panels c and d show reactive COP and head kinematic behavior, respectively. All four panels show single-subject data for the high uncertainty (circles) and low uncertainty (diamonds) conditions, as well as their corresponding means and standard errors. Dashed lines represent the baseline value as this was obtained during a quiet stance block with no perturbations. The * indicates $p < 0.05$ to tests against baseline values.

guidance of posture gains importance. There was again no main effect of temporal uncertainty ($F_{1,8} = 1.089$, $p = 0.327$, $\eta^2 = 0.037$), nor an interaction ($F_{2,16} = 0.642$, $p = 0.539$, $\eta^2 = 0.024$).

Discussion

We examined whether tactile sensitivity on the lower limb is modulated by feedback processing demands. To this end, we used an adapted version of the classical moving room paradigm[38,39,43,44] and examined the temporal modulation of tactile sensitivity on the lower leg during standing, while preparing for and reacting to visual perturbations that occurred at moments of low or high temporal uncertainty. We measured tactile sensitivity on the lower leg at different times during this task. We demonstrate that feedback processing demands modulate tactile sensitivity, enhancing sensitivity at the moments around the onset of the reactive postural response. This demonstrates that tactile sensitivity on the standing leg is temporally tuned to the dynamics of the perturbation and the need to sample sensory feedback from the probed body part to allow for balance retention.

The increased tactile sensitivity on the lower leg after the onset of the perturbation indicates an upweighting of somatosensory feedback signals from the standing limb around that moment. This appears inconsistent with previous findings that found *reduced* tactile sensitivity right before and during single finger movements[41,45], reaching and grasping actions[16], or foot extensions[19]. This apparent discrepancy can be explained by differences in the task relevancy of the sensory information from the probed limb. In our study, somatosensory information from the lower leg is important to control posture, particularly around the onset of the reactive response. This

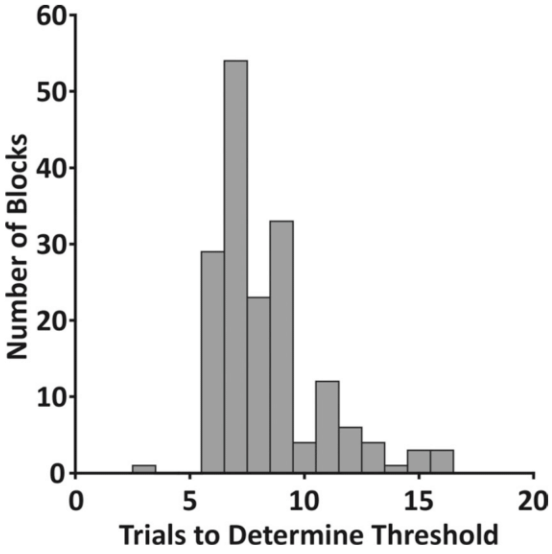

Fig. 2. Trials until threshold estimation. Histogram of the required number of trials to determine all valid detection thresholds over all participants. The histogram shows cumulative how many trials it took to estimate the 173 detection thresholds obtained in all conditions of the experiment.

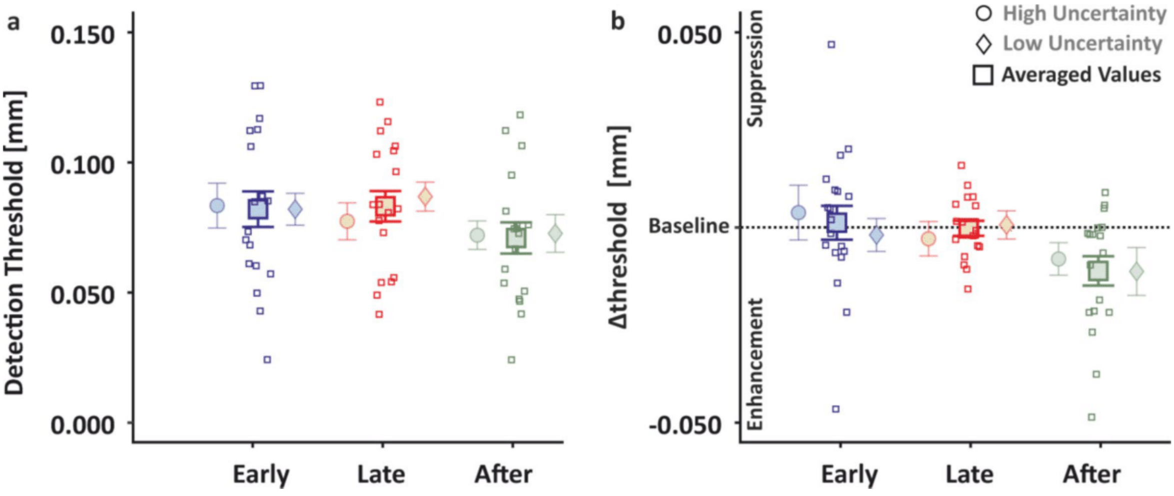

Fig. 3. Psychophysical results Experiment 1. Detection thresholds during the perturbation blocks. Comparison of raw (**a**) and normalized to standing (**b**) detection thresholds for the 3 time intervals of the high (circles) and low (diamonds) uncertainty conditions are shown shaded with their average presented in darker hues in-between (square). Single subject data (squares) for the average are depicted. Error bars with the means and standard errors are shown.

aligns with findings showing increased somatosensory-evoked potentials to tactile sensations from the foot sole shortly before initiating a step[20]. Such sensory modulation could reflect a reweighting of sensory signals based on their contribution to the underlying task, a phenomenon observed in various sensory modalities when maintaining an upright stance[23,24,46]. In our experiment, postural control relies on multiple sensory inputs, including visual, vestibular, and somatosensory signals. Since vestibular and somatosensory cues remain aligned, any conflict introduced by visual perturbation renders vision unreliable. This could prompt an increased reliance on other sensory channels, such as tactile input, to maintain balance. In a similar paradigm, a previous study reported that visual signals are up-weighted and perturbed proprioceptive signals from the leg are down-weighted when anticipating the avoidance of an approaching ball[25]. Though this might appear as inconsistent with our results, it is noteworthy that the down-weighting of proprioceptive inputs referred to Achilles tendon vibration signals that caused illusory postural sway, and that down-weighting such signals may be beneficial when maintaining balance. The modulation of tactile input from our participants' lower leg might also be related to the perceived threat related to the upcoming collision and the retention of body balance. For instance, improved tactile sensitivity around the time of the postural response might be caused by increased feedback

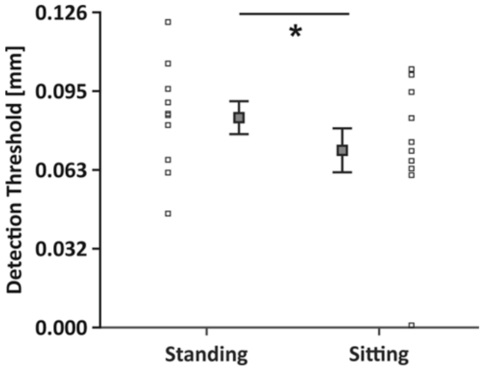

Fig. 4. Tactile perception between standing and sitting. Comparison of raw detection thresholds between standing and sitting. This graph shows the detection thresholds for (quiet) standing (left) and sitting (right) baselines. Single subject data is depicted with squares, whereas averages and standard errors are shown with squares and the respective error bars. * indicates $p < 0.05$.

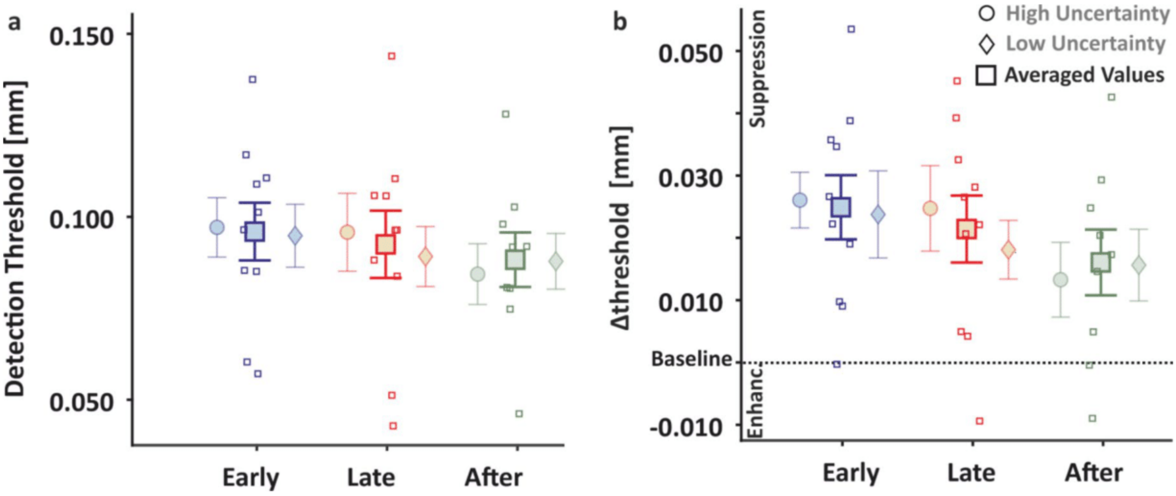

Fig. 5. Psychophysical results Experiment 2. Detection thresholds during the perturbation blocks. Comparison of raw (**a**) and normalized to sitting (**b**) detection thresholds for the three time intervals of the high (circles) and low (diamonds) uncertainty conditions are shown shaded with their average presented in darker hues in-between (square). Single subject data (squares) for the average are depicted. Error bars with the means and standard errors are shown.

processing associated with fear of the approaching wall, a possibility that would align with research on threat-induced modulation of tendon reflexes[21,47]. However, it is unlikely that this factor played a major role in our study, as participants were not only told that the wall would not hit them, but they likely learned after a few trials that the wall would not make contact with them. Taken together, we suggest that the sensorimotor system can flexibly up- and down-weight somatosensory signals depending on how reliable information they can provide for postural state estimation.

We also examined the effect of temporal uncertainty related to the moment when the visual perturbation was triggered. There is evidence that sensorimotor uncertainty can influence the strength of tactile sensitivity[14,48,49]. Here we explored if low temporal uncertainty about the onset of the perturbation would lead to stronger reliance on predictive control when postural demands increase. Although we found anticipatory postural behavior before perturbations of low temporal uncertainty, especially reflected in a reduction of the COP sway, we have no evidence that tactile sensitivity was influenced as well. We cannot exclude the possibility that the uncertainty about the onset of the perturbation was too small to impact tactile perception since the general trial structure of the two perturbation conditions was comparable. Alternatively, the variance in the perception data could be too high to detect meaningful changes, but different between the two uncertainty conditions. One factor contributing to the variance is that participants were allowed to either stand with or without socks on the force plate. As the type of footwear was kept constant across condition, this should not have influenced our results, but it might have impeded the detection of the uncertainty effect. Temporal uncertainty of the perturbation may have also influenced the between-subject-variance through anticipatory effects, such as a reduction in variance under low uncertainty. However, the observed variances appeared comparable across conditions and experiments.

Interestingly, in Experiment 1, tactile sensitivity during standing was not different between trials involving perturbations and those without (i.e. quiet stance). This indicates that standing upright already leads to increased tactile detection thresholds. Indeed, when compared to sitting in Experiment 2, tactile sensitivity during standing was significantly reduced, in line with previous findings that assessed tactile sensitivity on the foot sole[42]. Tactile suppression during upright stance may stem from one or more sources. One possibility is that muscle activation or changes in leg position altered skin stretch by affecting subcutaneous volume, which may have changed the skin's mechanical properties around the probed area and reduced tactile sensitivity[50]. For instance, skin deformation is known to influence tactile perception with higher deformation reducing tactile perception thresholds[40]. It is also possible that backward masking from the activation of the lower leg muscles, as well as the pressure on bones, and the tension of ligaments, tendons, and muscle spindles, increased sensory noise and thus made the brief vibrotactile probes less conspicuous. Indeed, standing itself is accompanied by an oscillatory movement[51]and postural adjustments[52]. When the stance is less stable e.g., the base of support is reduced, the activity of the lower leg muscles increases[53] and this increase in peripheral activity may mask the probing tactile stimuli[9,2]. However, so far there is no clear evidence that increased force production and hence muscular activity per se can modulate tactile suppression[10].

The sitting baseline occurred always at the end of the experimental procedure. This might render the reduced tactile sensitivity during standing as a by-product of improved tactile detection performance at the later (sitting) baseline simply due to practice. This could lead to lower detection thresholds towards the end of the experiment compared to the preceding standing tasks. This is unlikely in our experiments for two reasons. First, the standing baseline tasks that were presented at the end of Experiment 1 did not yield lower detection thresholds than the earlier presented perturbation tasks. Thus, the lower detection thresholds during sitting, which was the last block in Experiment 2, are unlikely to arise simply because of a longer exposure to the tactile task. Second, tactile detection thresholds, at least on the hand, do not differ between sessions separated by up to 30 min[15]. All in all, we have no evidence that the reported effects may be caused by a possible improvement in tactile detection over the course of the experiment.

Our kinematic results demonstrate small but systematic anticipatory behavior prior to the perturbations when temporal uncertainty was low. Unsurprisingly, there were no anticipatory adjustments prior to the perturbation of high temporal uncertainty. This is in line with previous work showing anticipatory behavior prior to predictable perturbations[25,54]. The anticipatory effects were mostly evident in the COP, while the head kinematics followed a similar but more variable pattern. This might be due to the sensorimotor system prioritizing the stabilization of the head over the trunk, as head stabilization is a common biological strategy. Stabilizing the head could reduce transformations of the sensory signals triggered during head movements or could provide a stable reference frame for the task at hand[55]. We also confirmed that participants react to new visual information by compensatory COP and head adjustments in the direction of perturbation evident after the onset of the room's motion, and independently of its temporal uncertainty in line with previous literature[38,44]. The reactive amplitudes are rather small and well within the base of support, but it is important to note that our participants had a narrow base of support (i.e., feet close together), which would make it disadvantageous to exert large COP excursions that could lead to postural instability and possibly loss of balance. Indeed, when the base of support induces greater postural instability, body reactions have much smaller amplitudes[31].

Together, our results demonstrate dynamic temporal modulation of tactile sensitivity on the lower limb when maintaining whole-body balance around visual perturbations and broaden our understanding of tactile sensory integration into postural control. The temporal tuning of tactile sensitivity when anticipating and reacting to a visual perturbation provides evidence for the idea that tactile sensitivity is dynamically modulated to the feedback demands. This upweighting of sensory feedback signals can lead to improved tactile sensitivity on a moving body part when somatosensory feedback signals from that part gain relevance for the sensory guidance of the movement.

Understanding the processing of tactile information in uncertain environments can be leveraged to assess and monitor an individual's ability to control posture. Recognizing the dynamic nature of tactile perception, rather than categorizing it as merely sharp or poor, provides a deeper insight into postural instability. Our results expand the set of studies showing that tactile sensitivity can be modulated during an action [e.g.[14–16,18,20], especially when feedback signals from the probed limb are important for the task, suggesting that tactile modulation around human movement is a dynamic process.

Limitations of this study

Even though there were anticipatory behaviors before the low uncertainty perturbation and no adjustments before the high uncertainty perturbations, we did not detect differences in tactile sensitivity between these two conditions. We assume that the uncertainty was large enough to cause small postural adjustments but too low to elicit measurable changes in tactile sensitivity. Another limitation relates to the origin of the tactile modulation. While we demonstrate that tactile sensitivity is dynamically modulated in both experiments, our experimental paradigm cannot pinpoint the exact underlying mechanisms behind this phenomenon. We describe possible explanations for this phenomenon in the Discussion.

Due to the low spatial specificity in the modulation of tactile perception[56] we were able to probe tactile perception on the lower leg. It is possible that the observed effect on increased sensitivity just before reactive adjustments would be even stronger and an anticipatory increase in tactile sensitivity could be observable when probed on the foot sole as done in other studies[20]. However, our device did not allow for such testing, opening an interesting avenue for future research.

Method details

Experiment 1

Participants and apparatus

We recruited 20 participants (24.4 ±4.8 years old; range: 19–39, 11 ♀ 9 ♂) for a one-session virtual reality experiment. One additional participant was recruited but did not finish data collection due to circulatory problems. Participants were free from any known neurological or musculoskeletal issues at the moment of the experiment and had normal or corrected-to-normal vision. All participants signed an informed consent. The study was approved by the local ethics committee of the Justus Liebig University Giessen. All methods were carried out in accordance with the "World Medical Association Declaration of Helsinki" (2013, except for § 35, pre-registration)[57]. At the end of the experiment, participants received for their efforts either 8€/hour or course credits.

A custom-made vibrotactile stimulation device (Engineer Acoustics Inc., Florida, US), which will be referred to as a "tactor", was attached to the skin area over the *musculus gastrocnemius lateralis* of the participant's right calf. It comprises a small housing (22 × 45 × 5 mm) and a round actuator (6 mm in diameter) that can generate vibrotactile stimuli of fine-grained duration, frequency, and amplitude (for vibrations of 250 Hz, this is between 0.00316 and 0.632 mm). This tactor was fixed at 3 cm medial of 2/3 of an imaginary line connecting the heel with the *caput fibulae* using kinesio tape. Thus, the tactile device was fixed on that specific area to serve as proxy of tactile signals when maintaining upright stance, considering that previous works has demonstrated that tactile input from the lower leg can provide important signals for postural control[36]. Compared to the foot sole or the Achilles tendon, this area is low in skin deformity which is a known cofounder of tactile perception[40]. With additional tape, care was taken that loose wires or clothing could not be mistaken as vibrations and that they would not hinder the performance of the task. While surface vibrations have been shown to modulate the function of the Golgi tendon organs and muscle spindles, their effect is likely minimal due to the high stimulation frequencies and low indentation amplitudes involved[58,59]. Furthermore, these alterations in afferent signalling should not interfere with the detection of tactile input from the surface.

Participants stood barefoot or with their socks on having their feet closed together on a force plate (AMTI, Massachusetts, US) that sampled the center of pressure (COP) at 300 Hz. They also wore a head-mounted display (HTC Vive Pro Eye, Taiwan) that presented a virtual environment and sampled translatory movements at a rate of 90 Hz. Participants were then immersed in a 3 × 3 × 6 m (width, height, depth) room with black and white striped side walls and a grey front wall. At 1.85 m above the floor, a circular fixation point with a 60 cm radius was presented (Fig. 6). The virtual environment was a custom-made Unity version 2021.3.4f1 (Unity Technologies, San Francisco, US) build. Kinematic and ground-reaction force data were synchronized using Vicon Nexus 2.11 and streamed into Matlab via the Vicon DataStream SDK 1.11 (Vicon Motion Systems, Oxford, UK). The Unity environment and headset data were synchronized by transmitting a trigger via LabStreamingLayer 1.14, achieving a latency of less than 0.1 ms on a local machine.

Procedure

The experiment consisted of five separate blocks of trials, each lasting 7 s. The first block was always composed of 30 training trials. Here, a countdown (3, 2, 1) appeared above the fixation point on the front wall, with each digit presented for 0.75 s. At the end of this countdown, a visual perturbation occurred, which consisted of the complete room moving in such a way that the front wall approached the participant with a velocity of 3 m/s for 5 m. Thus, the movement of the room toward the participant lasted for 1.67 s. The room size and motion were based on a previous study designed to elicit postural sway in participants[44]. After each trial, the room instantly recovered back to its original configuration. After this training block, two perturbation conditions were presented in a random order across participants. In each of these two blocks, the room could be perturbed at a moment of low or high temporal uncertainty. In the low uncertainty condition, trials started with a fixed delay of 0.75 s after the experimenter pressed a button, followed by a 2.25 s period of countdown, and the visual perturbation occurred immediately after that countdown. In other words, the perturbation was expected based on the presented countdown and it always occurred 3 s after the onset of the trial. In the high uncertainty condition, a trial would start without a countdown, and the perturbation would occur within a random moment between 2.25 and 3 s from the beginning of the trial. The absence of the countdown and the 0.75 s random delay increased the uncertainty about the exact moment of the perturbation onset. Everything else, including the velocity of the room's movement, were identical between the two levels of uncertainty. These resulted in a difference in the uncertainty of when the perturbation would occur between these two conditions, while also allowing us to capture the same time window during which the countdown appeared. Thus, we could examine possible anticipatory sensorimotor responses prior the perturbation in both perturbation conditions. Upon completion of these two perturbation conditions, two blocks followed where we assessed baseline sensory and motor performance: one block with and another block without a visual countdown, but importantly both blocks without any visual perturbation. In other words, these two baseline conditions were identical to the two perturbation conditions but now the virtual room never moved. The order of the two baseline conditions was identical to the order of the perturbation conditions, and this order was randomized across participants. Participants were explicitly informed prior to the onset of each block about the condition that they would be exposed to. In all blocks, participants were asked to fixate the fixation point at the center of the front wall at all times with their head in a natural configuration.

To probe tactile sensitivity, we delivered a brief (50 ms, 250 Hz) vibrotactile stimulus of varying intensities at the skin of the participants' right lower leg, over the calf muscle. The stimulus was presented at various moments during each trial, and participants had to verbally report whether they felt a vibration or not. This tactile stimulus is not relevant for the postural task, but is used as a proxy to assess tactile sensitivity; a procedure commonly applied in previous work[1,16,18]. In the two perturbation conditions, the probing tactile stimulus was delivered at a

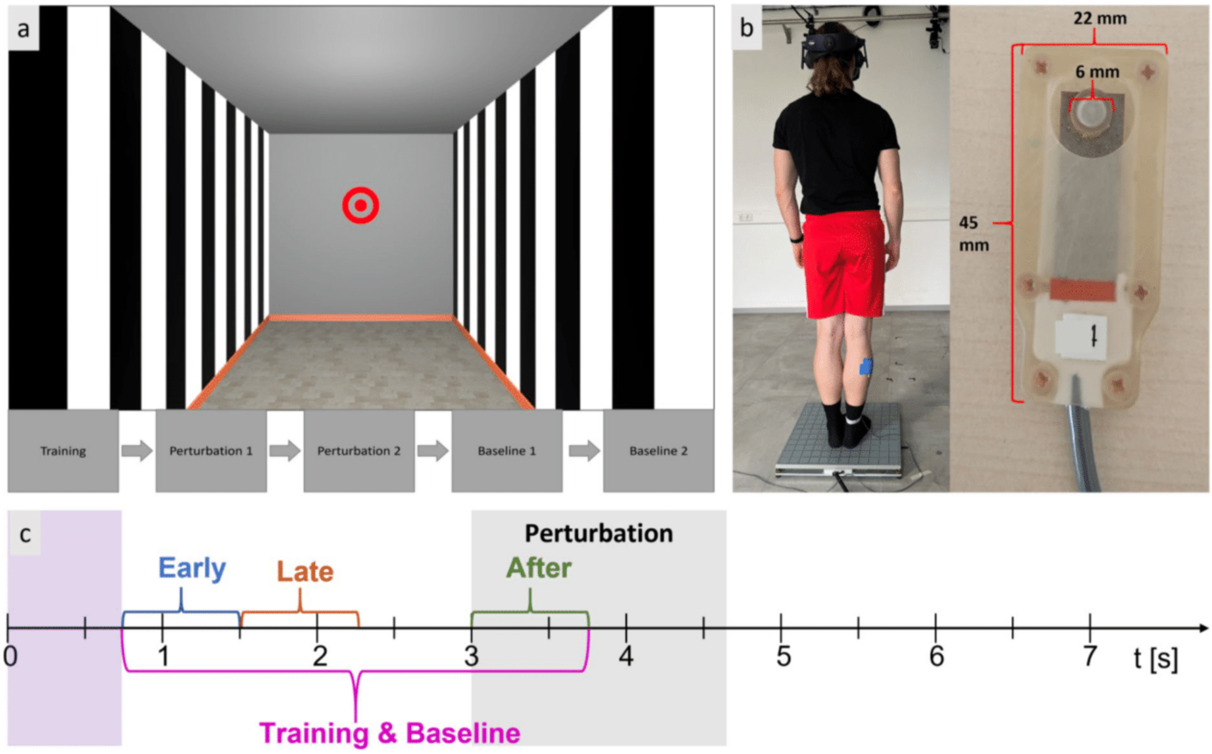

Fig. 6. Experimental setup. (**a**) Depiction of the virtual environment as seen from the participants with the block order below. The red circular fixation point appears at the front wall of the virtual room. (**b**) Setup in the lab with a photo of the tactor and its size in mm. (**c**) Schematic timeline of a single trial of the perturbation condition. The probe tactile stimulus in the two perturbation blocks could be presented at one of three possible intervals: "early" (blue), "late" (brown), and "after" (green), whereas in the baseline and training conditions, it could be presented at any moment during a single interval (purple). The onset of the perturbation is depicted here as starting at the 3rd second of the trial, but this could vary in the condition with the high uncertainty perturbation. The duration of the perturbation is indicated by the grey area.

random moment during one of three possible intervals relative to perturbation onset: two at the pre-perturbation period ("early": −2.25 to −1.50 s, and "late": −1.50 to −0.75 s) and one at the post-perturbation period ("after": 0.00 to 0.75 s; Fig. 6). We presented 30 trials at each of these three intervals in a randomized order, for a total of 90 trials per perturbation block. These three intervals were chosen based on the following considerations: tactile sensitivity during the "early" interval should be mainly unaffected by predictive mechanisms. The "late" interval should test whether predictive processes associated with the onset of visual perturbation will tune tactile sensitivity differently in the low and high uncertainty conditions. Finally, the "after" timepoint should cover any modulation that is primarily caused by the visual perturbation itself and the motor reactions.

In each of the training and two baseline conditions there was a single time interval during which the tactile probe could be presented: for the training and baseline condition with the countdown the stimulus was presented between 0.75 and 3.75 s, whereas for the baseline condition without the countdown it was presented between 0 and 3.75 s, always relative to the onset of the trial.

The intensity of vibration in each trial was determined using a QUEST algorithm (Psychtoolbox Version 3.0.18). As a Bayesian approach, the QUEST algorithm uses prior knowledge to estimate the parameters of a psychometric function. As the model function we used a Weibull distribution because it can represent a wide range of response patterns. We chose a β of 3.5 for the distribution which is the suggested value for 2 AFC tasks in the QUEST algorithm[60]. The prior mean and standard deviation for the training block were estimated from a pilot study where participants just stood with their feet closed (N= 16, exposed to 50 stimuli of varying intensities, presented at the skin over the calf muscle of the right leg). We used the mean of the estimated probability density function as probe intensity for the next trial. For all the other conditions we used the estimated threshold of the training block as prior mean[60,61].

In each trial, participants were instructed to verbally report whether or not they felt a vibration. They were instructed to immediately respond once they felt a vibration to avoid memory effects, but they were also explicitly asked to respond after the trial ended if no answer was meanwhile given. These verbal responses were then registered by the experimenter via button presses to a computer, which induced a short delay (0.5–1 s) between trials. To prevent fatigue, participants could have a break after every trial on request. Breaks of ~ 1 min were enforced every 30 trials and longer breaks of ~ 5 min were introduced after 90 trials. During these longer breaks, participants were required to sit and were allowed to remove the headset. This resulted in a duration of around

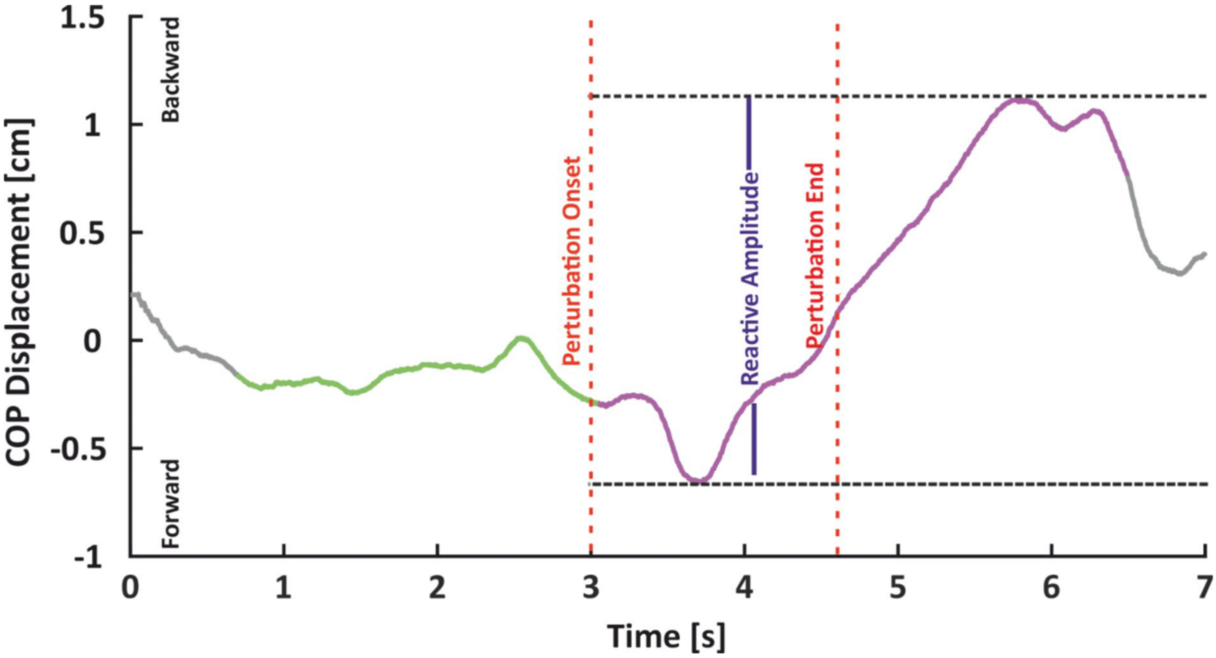

Fig. 7. Exemplary kinematic data. Temporal profile of the center of pressure (COP) time course in the antero-posterior direction of a low uncertainty trial. The time window of perturbation (red dashed lines), the anticipatory period (green path), the reactive period (purple path), and the reactive amplitude (blue solid line) are depicted.

20 min for each perturbation block, with a total experimental time of 90 min. Trial control, data acquisition, and data analysis were handled by custom-made Matlab R2021a software (The Mathworks, Massachusetts, US).

Data analysis

The COP and headset translational data were analyzed only in the anterior-posterior (negative to positive values, respectively) direction as the visual perturbation happened in this direction. In a first step, we excluded trials from all kinematic and psychophysical analyses with data that were continuously missing for at least 100 ms (1.2%; only COP data were ever missing). Afterward, we normalized every sample of each trial to the average position of the first 0.5 s of that trial, which we consider as a period of quiet stance because there was nothing happening to the room. The resulting normalized data was corrected for outlier data points by replacing values with a displacement larger than 15 cm with no value (this only affected COP data), and then smoothed utilizing a symmetric moving average with a window size of 100 ms.

Anticipatory behavior were quantified as the maximum absolute COP and head amplitude during the last 2.25 s prior to perturbation onset, that is the time window from the first possible vibrotactile probing until reactive movements could appear. To quantify reactive kinematic behavior we first determined the maximum positive (posterior) COP and head displacement during the first 3.5 s following the onset of the perturbation. This corresponds to about twice the perturbation duration. Determining the maximum positive COP and head position values to quantify motor responses was important because any reaction to the perturbation would result in the body leaning backward and thus to a positive COP and head position value. We then quantified reactive kinematic adjustments of the COP and head as the difference between their maximum value and their respective minimum that occurred between the perturbation onset and that maximum (see Fig. 7). We calculated both components for every trial of each subject and averaged across all trials for each uncertainty level. Both of the previous measures were normalized with respect to the values calculated from their respective baseline periods (quiet stance) to account for individual differences in standing. Thus, values greater than zero indicate larger displacements during the perturbation blocks relative to the respective baseline.

We determined tactile detection thresholds for each condition and participant. This was quantified as the first trial after which the probe stimulus intensity recommended by the QUEST did no longer change value. It is important to note that our device accepts only integer values as inputs for the tactile stimuli, but the values recommended by the QUEST could also include decimals. In these cases, we always rounded the suggested value to the nearest integer. Thus, although the QUEST suggested slightly different intensities in the trials after the detection threshold was determined, we presented the same stimulus intensities due to rounding. We expected some fluctuation in the responses to those trials due to natural randomness in detecting stimuli around one's own detection threshold. For this reason, we considered detection thresholds as invalid if participants gave the same (detected or not-detected) response in the remaining trials after the detection threshold was determined. The thresholds of those blocks (4.2%) as well as the corresponding kinematic data were excluded from further analyses. To quantify tactile modulation during perturbation relative to quiet stance trials while also accounting for individual differences in tactile sensitivity, we subtracted each participant's baseline detection threshold from their threshold obtained at each time interval of the respective perturbation block (Δthreshold), a procedure in line with previous work[10,13]. To closer align the kinematic with the perceptual results we included in the kinematic analyses of each condition and participant only those trials that were used to estimate the associated detection thresholds.

Statistical analysis

We first examined whether anticipatory behavior was evident prior to perturbation compared to baseline by testing if the maximum displacement in COP and head kinematics during the anticipatory period deviated from the respective values during quiet stance. Because we subtracted the maximum displacement in baseline from the respective value in the perturbation blocks, we quantified possible effects by using one-sided one-sample t-tests against zero for the low uncertainty (based on the directed hypothesis) and two-sided t-tests for the high uncertainty condition (based on the undirected hypothesis). Similarly, we tested whether the reactive component in each perturbation condition deviated from zero (i.e. baseline) using one-sided one-sample t-tests.

To first explore possible modulation of tactile sensitivity during the perturbation blocks relative to baseline, we submitted the obtained Δthreshold values to six separate two-sided one-sample t-tests against zero (i.e. baseline). Our main interest was whether tactile perception would be temporally tuned while anticipating and reacting to a perturbation. We also explored whether there would be any effects of the temporal uncertainty of the perturbation. To test for possible effects of the time interval of tactile probing ("early", "late", "after") and the type of perturbation (low vs. high uncertainty) on tactile sensitivity, we used a 3 × 2 repeated measure ANOVA. Significant main effects were explored with post-hoc t-tests, with p-values corrected for multiple comparisons wherever necessary using the Holm procedure, and with all t-values reported as absolute values. The type one error threshold was set to 0.05 and effect sizes are reported as η^2 following the calculations and recommendations of Correll and colleagues[62]. Statistical analyses were conducted in JASP version 0.17.1 (University of Amsterdam, Netherlands). Datapoints in any of the 6 experimental or 2 baseline conditions that were outside of the 3.5 interquartile range were excluded from the statistical analysis of that condition as outliers (< 1% for kinematic and 0% for psychophysical data). If any baseline value was excluded, the three values in the associated perturbation condition were also excluded since normalization was impossible.

Experiment 2

In Experiment 1 we examined the temporal modulation of tactile sensitivity when coping with visual perturbations of high or low temporal uncertainty during upright stance. To this end, we compared tactile perception when standing and being confronted with a perturbation to when standing without having to cope with any perturbation. However, standing itself may already influence tactile sensitivity on the leg, for instance by masking feedback signals, or by changes in skin and muscle-related properties on the probed body part. To account for such possibilities, we conducted Experiment 2, where we examined whether tactile detection thresholds at the lower leg differed between quiet stance and sitting. We further examined whether tactile modulation followed similar patterns to those observed in Experiment 1.

Participants and experimental design

We recruited 12 new participants, with two of them not finishing data collection due to circulatory problems or incompliance with task instructions. Thus, our final sample was 10 participants (25.3 ± 4.0 years old; range: 21–32; 9 ♀ 1 ♂) who joined a one-session experiment. The procedure was almost identical to Experiment 1, but participants now performed six blocks of trials: a training block, two perturbation blocks, two standing baselines, and after these, an additional sitting baseline. During this sitting baseline, participants wore the head-mounted display and sat relaxed on a chair with their knees flexed at ~ 90° and both feet touching the floor. In this sitting baseline, participants performed 30 trials that were constructed identically to those in the other two standing baseline blocks. In all six blocks of Experiment 2, participants saw the same room as in Experiment 1. The experimental procedure and analyses were identical to those reported for Experiment 1, except for the details mentioned below.

Data and statistical analysis

As we were interested in the modulation of tactile sensitivity by standing, we focused our analysis on tactile detection thresholds. In contrast to Experiment 1, detection thresholds obtained during the two perturbation blocks of Experiment 2 were now normalized with respect to the new sitting baseline, resulting once again in six Δthreshold values per participant. The analysis of the participants' responses after the detection threshold resulted in excluding 1.5% of the total detection thresholds and their corresponding kinematic data. Furthermore, and since we did not observe any differences in the two standing baselines in Experiment 1 ($t_{19} = 0.621$, $p = 0.542$, $\eta^2 = 0.005$) or Experiment 2 ($t_9 = 0.263$, $p = 0.798$, $\eta^2 = 0.002$), we now averaged across the two standing baselines thresholds for each participant.

A two-sided paired t-test was performed to test for differences between the standing and the sitting baselines. To further examine whether tactile detection thresholds increase during the perturbation blocks relative to the sitting baseline, we contrasted the six Δthreshold values against zero (i.e. baseline) with six separate one-sided one-sample t-tests. Additionally, we submitted the Δthreshold values to a 3 × 2 repeated measure ANOVA to investigate for main effects of the time of probing ("early", "late", "after") and of type of perturbation (low vs. high uncertainty) on tactile modulation, as in Experiment 1.

Key resources table

Resource	Source	Identifier
Software and Algorithms		
Matlab 2021a	MathWorks	https://de.mathworks.com/products/matlab.html
Vicon datastream SDK	Vicon Motion Systems	https://www.vicon.com/software/datastream-sdk/
QUEST	Psychtoolbox 3.0.18	http://psychtoolbox.org/
JASP 0.17.1	JASP	https://jasp-stats.org/
LabStreamingLayer	LabStreamingLayer	https://github.com/sccn/labstreaminglayer
Unity 2021.3.4f1	UNITY	https://unity.com/
Hardware		
Tactor	Engineering Acoustic Inc.	https://eaiinfo.com/
Forceplate	Advanced Mechanical Technology Inc.	https://www.amti.biz/
VIVE Pro Eye	HTC Corp	https://www.vive.com/de/

Data availability

Behavioral and psychophysical data are publicly available after acceptance at https://osf.io/jdzwa/. For further information or data requests please correspond to Fabian Dominik Wachsmann (Fabian.Wachsmann@psychol.uni-giessen.de).

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3 Publication 3

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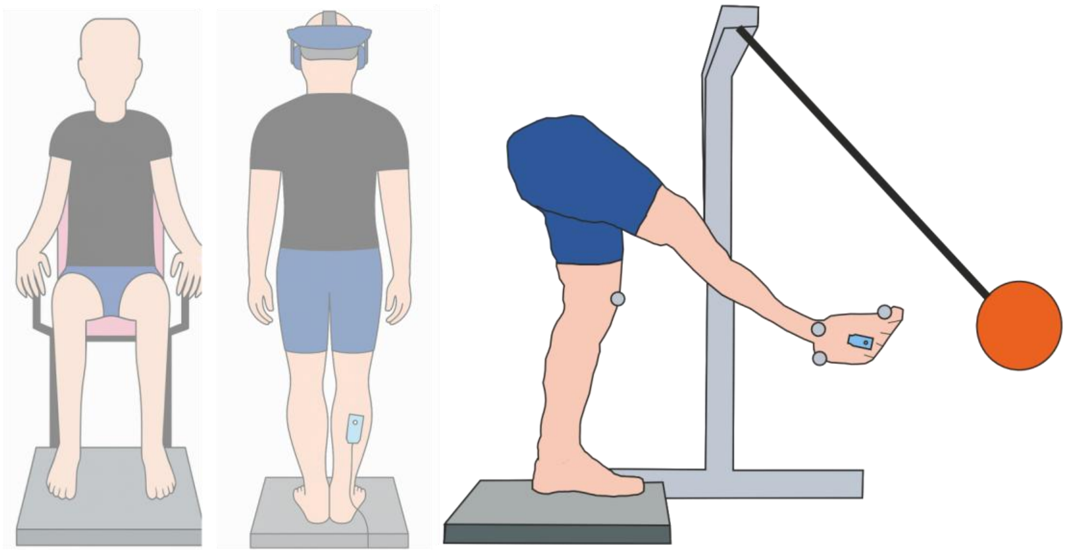

Modulation of tactile sensitivity in the lower limbs during goal-directed movements

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Abstract

Tactile sensitivity drops in a moving than static limb due to a combination of central, predictive mechanisms and peripheral effects. This suppression is dynamically modulated during movement, as shown during upper-limb actions, yet little is known about its implication during complex lower-limb movements. We investigated tactile sensitivity during naturalistic kicking by delivering vibrotactile probe stimuli to the balancing and kicking feet at different movement phases. In Experiment 1, participants kicked a suspended ball while tactile sensitivity was probed at movement *onset*, mid-*swing*, ball *contact*, and *after*-contact. Results revealed distinct modulation patterns in each foot. When transitioning from bipedal to unipedal stance, tactile processing at the balancing foot was particularly suppressed but at the kicking foot it improved, suggesting concurrent modulation across the two legs depending on their motor function. Tactile sensitivity remained rather invariant at other time points, but was strongly suppressed on the kicking foot at the moment of ball contact. The strength of this suppression correlated with kicking speed, which could reflect either stronger predictive control or stronger peripheral processes that mask the vibrotactile probe. To test these, a new set of participants held their foot still while a ball collided with it at high or low speed. Suppression was greater with faster ball contacts, revealing that peripheral processes can modulate tactile processing. These findings show that lower-limb tactile sensitivity during goal-directed leg movements can be concurrently modulated across the legs, presumably reflecting an interplay between central sensorimotor processes guiding the movement and peripheral processes affecting sensitivity.

Keywords

Tactile Suppression, Tactile Masking, Sensory Integration, Postural Control, Kicking

Significance Statement

Tactile sensitivity is known to fluctuate during movement, but little is understood about how it is tuned during complex lower-limb actions. Using a naturalistic ball-kicking task, we reveal distinct modulation patterns in the balancing and kicking feet, showing that postural and guiding demands dynamically shape tactile sensitivity. We further demonstrate that the strength of tactile modulation is influenced by peripheral processes, such as tactile masking. These findings highlight that lower-limb tactile processing can be flexibly and concurrently modulated in the two legs during state transitions that impose different sensorimotor demands for complex natural behavior.

Introduction

Tactile sensitivity is typically reduced on a moving limb compared to when the same limb is resting. This suppression stems primarily from predictive mechanisms, in which motor commands anticipate future sensory states, leading to suppression of associated sensory feedback (Blakemore et al., 2000). This predictive process explains why self-produced sensations, like tickling (Blakemore et al., 2000) or the strength of self-applied forces (Shergill et al., 2003), feel weaker during active tasks. However, externally-generated sensations, which cannot be predicted based on motor commands, are also suppressed on a moving limb (Arikan et al., 2024; Fuehrer et al., 2022). This led to the idea that the suppression of externally-generated sensations arises from a general gating mechanism unrelated to prediction (e.g., Kilteni & Ehrsson, 2022). However, accumulation of findings demonstrates that suppression of externally-generated sensations reflects the integration of feedforward predictions with online sensory feedback (Fuehrer et al., 2022; Mouchnino et al., 2015). For example, tactile suppression during grasping is reduced when tactile input is important for object manipulation (Voudouris et al., 2019; Voudouris & Fiehler, 2022). Suppression is also temporally modulated during goal-directed arm movements (Colino & Binsted, 2016; Fraser & Fiehler, 2018), with recovered sensitivity when somatosensory feedback becomes critical (Voudouris & Fiehler, 2021). Tactile sensitivity can also change in the leg during whole-body actions, such as walking (Pearcey & Zehr, 2019). For instance, it can improve when preparing to avoid a visual perturbation (Wachsmann et al., 2025a) or just before initiating a step (Mouchnino et al., 2015), reflecting upregulation of task-relevant tactile input for postural stability. Overall, these results demonstrate the flexible, context-dependent modulation of tactile sensitivity during movement.

An important distinction between upper-limb and whole-body actions is that the latter require the retention of upright stance. This on its own requires a cascade of sensorimotor processes from multiple effectors to ensure a stable posture and the successful execution of the overarching body action. For instance, when retaining bipedal posture, the sensorimotor system should control sensory processing from two separate effectors (legs) that may sometimes even be exposed to different dynamics. One such example occurs during postural transitions, like walking or kicking, when the two effectors need to simultaneously coordinate the redundant degrees of freedom based on the available sensory information and feedforward predictions, to ensuring stable upright stance and successful performance.

Considering these, we are here interested in the regulation of tactile processing from both legs during postural transitions. We focus on ball kicking, which involves complex sensorimotor processes for both feet. The balancing foot supports posture, while the kicking foot executes a goal-directed movement. Performance is associated with balancing ability (Chew-Bullock et al., 2012) and a trade-off between speed and accuracy of the kicking leg (Kellis & Katis, 2007). Meanwhile, cutaneous and other sensory signals inform about postural disturbances (Peterka, 2002). We examined tactile processing in the balancing and the kicking foot during postural transitions, when each leg serves different functional purposes to foster successful behavior. We propose two main hypotheses. First, for the balancing foot, we expected reduced tactile sensitivity during the *swing* phase of the kicking foot compared to other moments because the transition from a stable bipedal to an unstable unipedal stance can reduce tactile sensitivity (Wachsmann et al., 2025b). Second, for the kicking foot, we predicted enhanced tactile sensitivity during the *swing* phase that would reflect uptake of somatosensory input to facilitate the guidance of the moving foot to the ball (Voudouris & Fiehler, 2021). We further hypothesized reduced sensitivity in the kicking leg at ball contact due to masking (Fraser & Fiehler, 2018). To examine this deeper, we tested whether the speed of a moving ball can modulate tactile sensitivity on a static leg at various times around ball-foot contact. Based on earlier research (Abramsky et al., 1971; Kirman, 1984), faster collisions should cause stronger suppression due to peripheral processes masking the sensations in a limited window around contact.

Methods Experiment 1

Participants and apparatus

We recruited 23 young (25.83 ± 3.69 years old, range: 21-36; height: 175.52 ± 10.23 cm; 8♀, 15♂) healthy participants. Participants were free from any known neurological or musculoskeletal issues at the moment of the experiment and had normal or corrected-to-normal vision. Upon their arrival at the lab, they provided their signed informed consent. At the end of the experiment, participants received either 8€/hour or course credits. The study was approved by the local ethics committee of the Justus Liebig University Giessen and was conducted in accordance with the "World Medical Association Declaration of Helsinki" (except for §35, pre-registration) ("World Medical Association Declaration of Helsinki", 2013).

Two custom-made vibrotactile stimulation devices (Engineer Acoustics Inc., Florida, USA), referred to as "tactors," were attached to the glabrous skin between the third and fourth metatarsal heads of both feet —an area known for its sensitivity to vibrotactile stimuli (Hennig & Sterzing, 2009). The tactors comprised a small housing (22 x 45 x 5 mm) and a round actuator (6 mm diameter) that can generate vibrotactile stimuli of fine-grained amplitude ranging from 0.00316 – 0.632 mm in steps of 0.00316 mm (Figure 1a). We used these tactors to generate brief tactile stimulations that served as a proxy to examine tactile processing from the stimulation site. This is based on findings and procedures from several previous studies that examined tactile sensitivity during upper-limb (Buckingham et al., 2010; Fuehrer et al., 2022; Voudouris & Fiehler, 2017, 2021) and lower body movements (Menz et al., 2006; Wachsmann et al., 2025a, 2025b). Care was taken to ensure that loose wires or clothing did not interfere with the perception of vibration or hinder task performance.

During the experiment, participants placed their left foot on a platform and kept it there. The position of each leg was recorded with reflective markers (spheres of 10 mm diameter) that were placed on certain anatomical landmarks of each leg. Specifically, for the kicking leg, the markers were placed at the malleolar fork, the lateral malleolus, and the first metatarsophalangeal joint (Figure 1a). For the balancing leg, the markers were attached at the knee cap, the *spina iliaca anterior superior,* and at the middle of the line connecting the previous 2 markers (Figure 1b). In addition, four reflective markers were placed on a foam ball (21 cm diameter, 290 g), which was suspended from a beam in front of the participant. The top part of the beam was positioned 115 cm above standing level, and the ball was suspended 1-2 cm above the standing level to enable free kicking. The variance in suspension level was due to the rope sometimes winding up and thus slightly shortening during several kicks. All ten markers were tracked at 300 Hz using eight Vicon Vero 2.2 (Vicon Motion Systems, Oxford, UK) cameras, with data captured and processed using Vicon Nexus 2.15 software. The marker data were streamed into MATLAB (version 2023b, The MathWorks Inc., Natick, Massachusetts, USA) via the Vicon DataStream SDK (version 1.12.0). A schematic depiction of the setup, including the positioning of the tactors and markers can be seen in Figure 1a-b.

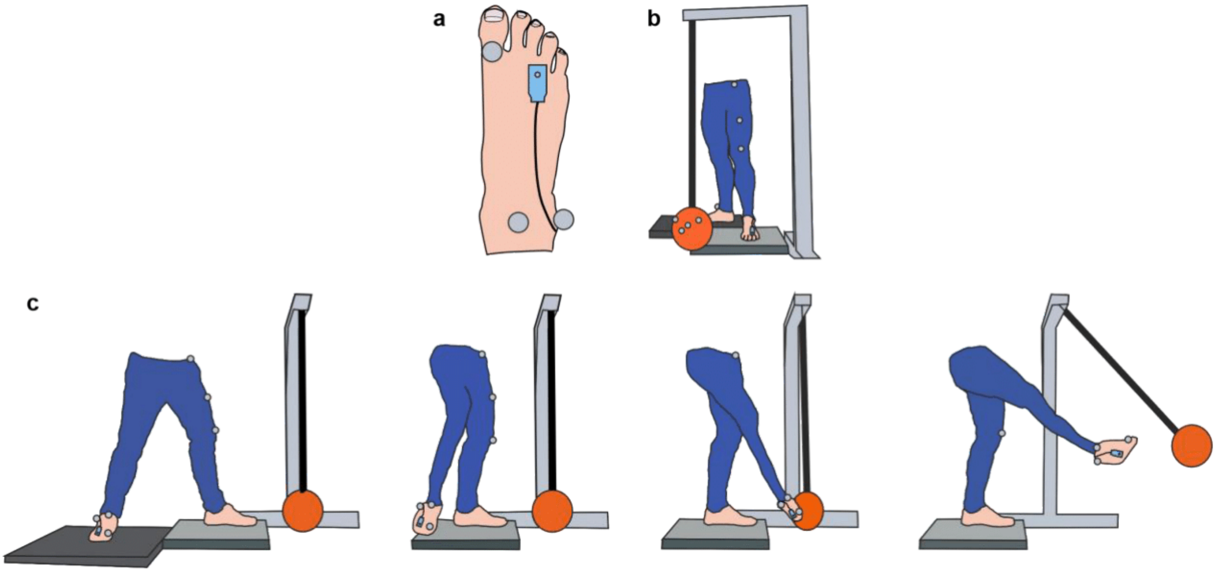

Figure 1: ***Setup Experiment 1.*** *(a) Top view of the right foot with the tactor placed at the metatarsophalangeal joint between the 3rd and 4th toes. (b) Experimental setup, with the ball suspended from a beam with the 4 markers attached to it and a platform where participants stood on. The three markers, as well as the tactile device, are depicted for the left leg. (c) Sketch of the starting position, mid-swing, ball contact, and after-contact time points (from left to right).*

Procedure

The experiment consisted of four main blocks: two baseline blocks to assess tactile sensitivity in each foot during rest, and two experimental blocks to assess changes in tactile sensitivity during kicking.

Before these four blocks, participants underwent a familiarization phase during which they got accustomed with the tactile stimuli and practiced the kicking trials.

During the familiarization phase, participants stood on the platform with their feet at shoulder-width apart. They performed five trials, each of which included a vibrotactile stimulus (50 ms, 250 Hz) at either the balancing (always left) or the kicking (always right) foot. The stimulus intensity ranged from weak (peak-to-peak amplitude: 0.00316 mm) to strong (peak-to-peak amplitude: 0.284 mm), allowing participants to become familiar with the sensations. All participants were able to detect at least one of these stimuli. After these five trials, participants held their kicking foot against the hanging ball, which allowed us to determine the minimum distance between the foot and the ball markers. This was important to later define the moment when the kicking foot contacted the ball (see below). Specifically, participants had to touch the ball with the medial side of their right foot, as if they were performing a kick. As soon as this was visually confirmed by the experimenter, the positional data from the markers on the foot and the ball were collected for 1 second. We then determined the median distance between the averaged positions of the right foot and of the ball markers over the recording. Participants then completed six practice kicking trials. They were instructed to take a kicking-ready stance, with the balancing foot in front and the kicking foot positioned further behind on another platform of similar height (Figure 1c). Tape markings were placed on the platforms to ensure consistent foot positioning between trials for each participant. In each trial, participants were asked to kick the suspended ball and attempt to replicate the same movement across all kicks. During the six practice kicking trials, participants also received high-intensity vibrations (0.632 mm) at three different time points: when lifting the kicking foot toward the ball, at ball contact, and 250 ms after ball contact. The first three trials involved vibrations at the balancing foot, and the next three trials included stimuli at the kicking foot. Each trial was initiated by the experimenter pressing a button followed by a brief tone after one second, indicating that the participant should execute the kick. The kick had to be completed within 15 seconds from the onset of the tone. The onset of movement was defined as the first moment when the average position of the markers on the kicking foot moved more than 1.5 cm from their starting position, which was defined as the average position of the foot markers during the 100 ms preceding the tone. Ball contact was detected when the Euclidean distance between the kicking foot and the ball was within 1.5 cm of the previously determined minimum foot-ball distance. This familiarization procedure lasted approximately 5 minutes.

After these familiarization trials, participants were randomly assigned to one of four possible sequences of blocks, each block assessing tactile sensitivity on one of the feet under a baseline and a kicking session. The order of the four blocks was randomized with the constraints that (a) the baseline blocks had to be presented sequentially either as the first or the last pair of blocks, and (b) the order of the tested feet was identical between baseline and kicking blocks. The four sequences were balanced across participants. Baseline measures were taken in sitting with both feet touching the ground. In each baseline trial, a tactile stimulus was delivered to the foot, and the experimenter asked the participants to verbally report whether they felt a vibration or not. The experimenter then logged the response to the host PC, and after a random delay between 2 and 3.5 seconds, a new tactile stimulation occurred, followed by the experimenter's question. The variable delay was introduced to minimize the temporal predictability of the stimulus. In each kicking trial participants had to first adopt the starting position. The experimenter then pressed a button that triggered an auditory go-cue 1 second later. This instructed participants to perform the kicking movement with their right foot within the next 15 seconds. A tactile stimulation occurred at one of four possible time points, which were fully randomized within each block. Three of these time points were identical to those used in the familiarization procedure: movement *onset*, ball *contact*, *after*-contact. The fourth time point occurred halfway through the *swing* phase of the kick (Figure 1c). This time point was estimated for each trial by calculating the swing movement time as the duration between movement onset and ball contact. We then calculated the average duration of the last five trials and used this as an estimate of the swing duration in the upcoming trial (e.g. Gertz et al., 2017; Arikan et al., 2021; Voudouris & Fiehler, 2022). This method provided robust estimates of movement times, resulting in a mean difference of 21 ± 21 ms between the intended and actual stimulation time for trials with stimulations planned during the swing phase (see Appendix 2 for a histogram). For the first five trials of each experimental block, we estimated the movement time based on the last trials of the practice kicks that were performed during the familiarization phase. For each of the two baseline conditions and for each of the four time points during the movement trials we presented 25 stimuli, totalling 250 trials per participant. This took about 45 minutes to complete. Participants could take breaks at any time during the experiment, but no one did.

The stimulus intensity for each trial was determined using a QUEST algorithm (Psychtoolbox Version 3.0.18; separate for each condition), which employs a Bayesian approach to estimate psychometric function parameters based on prior knowledge. This was done separately for each of the four blocks and separately for each participant. If suggested values were larger or smaller than those that the tactor could generate, we used the maximum (0.284 mm) or minimal (0.00316 mm) possible values, respectively. A Weibull function with $\beta = 3.5$ was used, as recommended for two-alternative forced choice (2AFC) tasks (Watson & Pelli, 1983). Prior mean and standard deviation estimates were based on a pilot study with young participants ($N = 16$), who were exposed to 50 stimuli of varying intensities while standing with their feet together. Lapse and guess rates were informed by another study on balance control during standing (Wachsmann et al., 2025b).

Data analysis

We determined the detection threshold for each condition and participant as the intensity of the tactile stimulus that was determined by the QUEST after the participant’s response in the last trial of the respective block. As mentioned above, and if necessary, this intensity was corrected to fit within the possible stimulation range of the tactor. We were primarily interested in assessing how tactile sensitivity on either foot is modulated during a kicking action. Therefore, to account for individual differences in tactile sensitivity, we normalized each participant’s detection thresholds of the kicking and the balancing foot during kicking blocks to the respective thresholds obtained during the baseline blocks. This resulted in four Δthreshold values, with higher values indicating higher thresholds during kicking than baseline trials (i.e. suppression).

If a resulting Δthreshold value in a single condition was lying outside the median ± 3 * interquartile range, the participant was excluded from the analysis using that parameter. Each of the 8 normalized conditions was checked individually. This resulted in excluding three Δthreshold values, each from a separate participant, from the following conditions: kicking foot *onset*, kicking foot *swing*, and kicking foot *after*-contact. Please note that if a Δthreshold is excluded, the whole participant could not be used for the ANOVA (see below), which would require that value. This resulted in three participants being excluded.

To visualize the leg kinematics, we first smoothed the positional data with a 33 ms (10 frames) moving average window to reduce high-frequency artefacts. Then we determined the speed of each leg separately by numerical differentiating the average positional data of the markers on that leg. We did so separately per trial and condition, and we then averaged across those trials to obtain two average speed profiles (one per leg) for each participant. We then averaged across the participants, and we present these averages starting from 1 second before the onset of the right foot's movement and until 1.5 seconds later. This is a time window that covers the preparatory and execution phases of the kick movement. In addition, we provide a time-normalized speed profile for each leg to further highlight the movement dynamics of each leg at the critical three time points of stimulation that occurred during the movement. To obtain the time-normalized speed profiles of each leg, we normalized the speed profile of every trial via linear interpolation to obtain a time course of 100 equal steps per trial, and then averaged across the 200 kicking trials of each participant.

Statistical analysis

Our main interest is whether tactile sensitivity on the balancing and kicking feet is temporally modulated during a kicking action of the right foot. To assess this, we conducted 2 separate one-way repeated measure ANOVAs, one per foot, with 4 levels (time points of stimulation). For the statistical analysis we used the Δthresholds. Main effects were explored with post hoc comparisons using paired t-tests (two-sided), corrected using the Holm procedure.

Results Experiment 1

Psychophysics

Baseline tactile sensitivity on the two feet is depicted in Figure 2a. As can be seen, detection thresholds appear somewhat lower in the right (kicking) than left (standing) leg, but this difference is not systematic, while the variability across participants is considerable, yet similar between feet. This is in line with previous findings that indicate substantial individual differences in tactile sensitivity (Kozłowska, 1998). Therefore, examining the relative change of the detection thresholds between kicking and baseline trials allows us to reduce the impact of these individual differences and focus on the temporal modulation of tactile sensitivity.

During kicking trials, tactile sensitivity was suppressed on both feet (Figure 2b), as all Δthreshold values were larger than zero (all $t >= 3.479$, all $p <= 0.002$, all $\eta^2 >= 0.116$). This is in line with previous findings showing that standing itself can lead to reduced tactile sensitivity (Wachsmann et al., 2025b). In addition, and most importantly, tactile sensitivity was temporally modulated both on the balancing ($F_{3, 66} = 3.604$, $p = 0.018$ $\eta^2 = 0.141$) and the kicking foot ($F_{3, 60} = 50.435$, $p < 0.001$ $\eta^2 = 0.716$). For the balancing foot, sensitivity was poorest during the *swing* phase compared to all other 3 time points ($t >= 2.524$, $p <= 0.049$, $\eta^2 >= 0.063$), but none of the other comparisons was systematic ($t <= 0.411$, $p = 1$, $\eta^2 <= 0.001$). For the kicking foot, we found clear differences between all time points of stimulation ($t >= 2.663$, $p <= 0.015$, $\eta^2 >= 0.042$). Specifically, tactile sensitivity increased during the *swing* phase, before declining at the moment of contact and recovering again after the end of the kick. It is remarkable that tactile sensitivity decreased on the balancing foot but increased on the kicking foot during the *swing* phase, suggesting a concurrent modulation of tactile processing at the two feet, presumably reflecting the differential sensory processing to complete the two separate functional tasks that each leg has to solve for successful behavior.

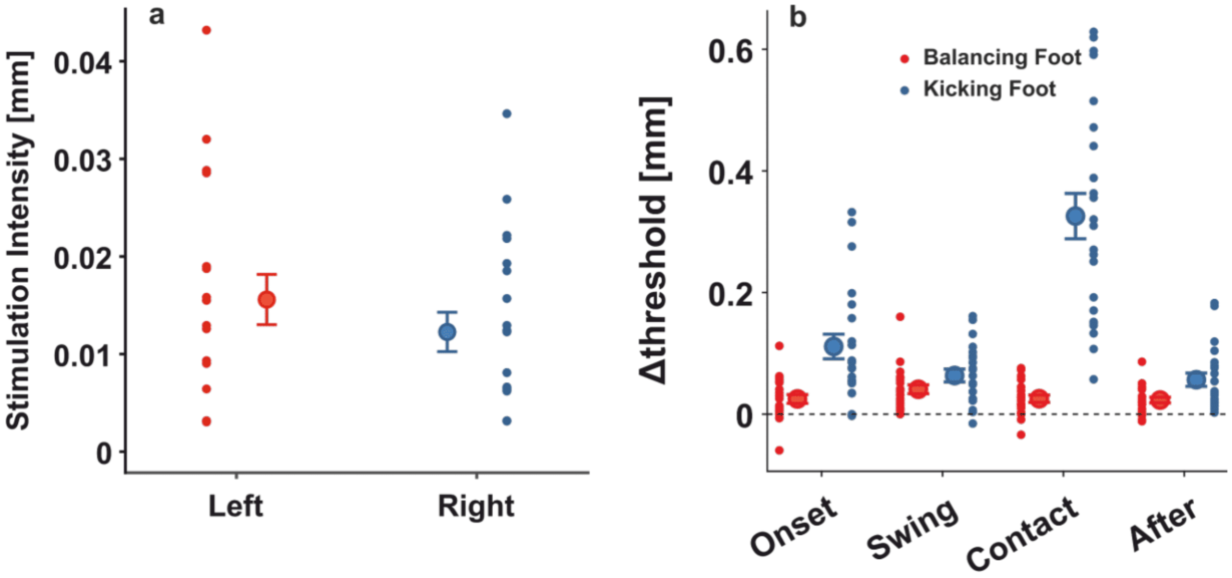

Figure 2: ***Temporal modulation of tactile sensitivity.*** *(a) Raw detection thresholds obtained for the left (red) and the right foot (blue) during rest. Note that the left and right feet are always the balancing and kicking feet, respectively, during the experimental blocks. (b) Normalized detection thresholds as function of the four stimulation time points. The dashed line indicates baseline level thresholds. For both panels, red data corresponds to the balancing and blue to the kicking foot. Single dots represent single subject thresholds, while circles with error bars represent the mean and standard error of each condition, respectively.*

Kinematics

Figure 3a illustrates the average foot speed across all trials and participants, with the moment of movement *onset* and ball *contact* being highlighted with the two vertical purple lines. Thus, the swing phase is the period between these two lines. Figure 3b presents the time-normalized speed of each foot during *swing* phase averaged across participants, thereby accounting for variability in swing durations due to different kicking speeds. Individual normalized graphs for each participant are available in Appendix 1.

As can be seen in Figure 3a, the action starts with the slow movement of the balancing leg, presumably indicating the postural adjustments that will enable the movement of the right leg. The speed of the kicking leg increased sharply ca. 500 ms later, reached its peak toward the end of the swing phase, and suddenly decreased its speed just before ball contact. This decrease in the movement speed appears consistent with patterns typically seen in goal-directed movements like reaching (Elliott et al., 2017). The speed of the kicking leg at the moment of contact ranged from 2157 mm/s (25th percentile) to 2579 mm/s (75th percentile), with a median of 2174 mm/s.

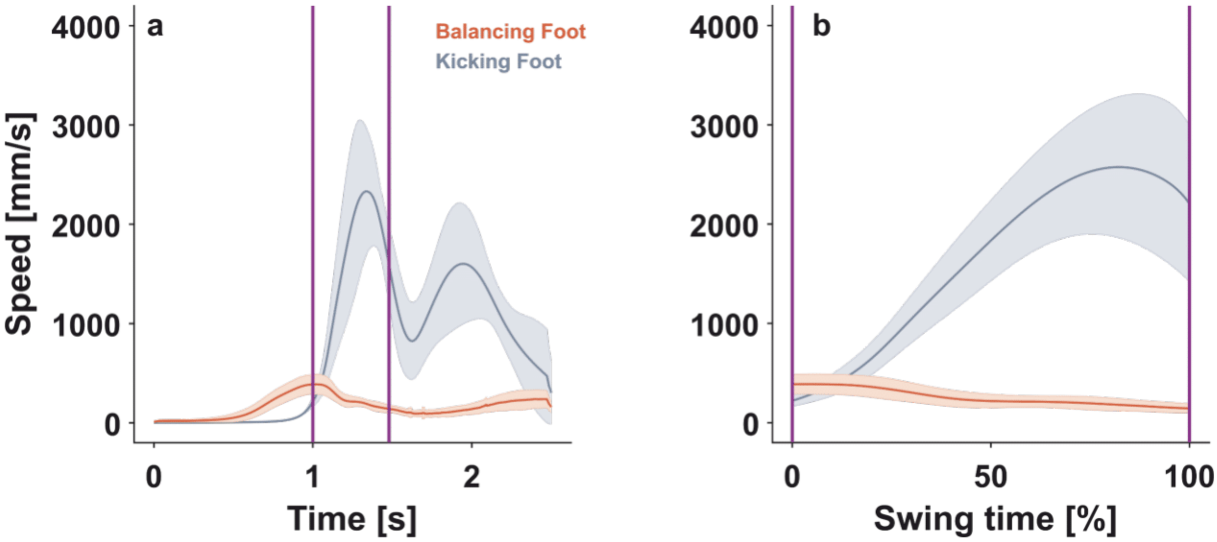

Figure 3: ***Kinematic results.*** *(a) Time-course of the balancing (red) and kicking (blue) foot speeds from 1 second before movement onset until 1.5 seconds after movement onset. (b) Time normalized time-course of both feet speed during the swinging phase. Time-courses are averages across participants, with shaded bands indicating standard errors across participants. The first and second purple vertical lines indicate the moments of movement onset and ball contact, respectively.*

Discussion Experiment 1

We examined tactile sensitivity on the two feet during a naturalistic ball kicking movement. We probed tactile sensitivity on both the balancing and kicking feet at four different time points of the action. First, we could replicate a previous finding that standing and the preparation of movement reduce tactile sensitivity on both feet compared to when simply sitting (Wachsmann et al., 2025a). For the balancing foot, we hypothesized that tactile sensitivity would decrease during the *swing* phase of the kick relative to all other moments of the action, based on previous findings showing that a rapid rise in balancing demands can reduce tactile sensitivity (Wachsmann et al., 2025b). Our findings confirm this hypothesis, providing further evidence for the idea that increased balancing demands when shifting from the bipedal to unipedal stance can compromise tactile sensitivity. This is at odds, though, with previous work showing improved tactile sensitivity in the leg shortly before a postural response to secure body balance, either when avoiding a visual perturbation (Wachsmann et al., 2025a) or when shifting weight to the balancing leg before initiating a step (Mouchnino et al., 2015). Therefore, the actual role of balancing demands on tactile sensitivity needs further investigation.

For the kicking foot, we hypothesized that tactile sensitivity would increase during the *swing* phase, driven by the need to guide the moving foot to accurately hit the ball. This is based on previous work from upper limb goal-directed action that showed improved tactile sensitivity on a reaching arm at moments when sensory guidance of the movement was more important (e.g., Voudouris & Fiehler, 2021; 2022; Fraser & Fiehler, 2018). However, it is also possible that tactile sensitivity would be reduced during the *swing* phase, because the high movement speed of the stimulated limb might lead to tactile suppression (Cybulska-Klosowicz et al., 2011). Our results do not lend evidence for this latter possibility, as sensitivity on the kicking foot was highest during the *swing* phase. This suggests that the possible effects of movement speed on tactile suppression may be less consistent. A striking finding of this experiment is that the detection thresholds in the kicking foot at ball *contact* were both highly elevated and rather variable across participants (see Figure 2b). These might arise from differences in kicking performance, particularly the variability in kicking speeds we observed in our data. A correlational analysis between kicking foot speed at the moment of ball *contact* and the strength of suppression (Δthreshold) from trials where the kicking foot was probed at that moment revealed a significant positive relationship ($r = 0.467$, $p = 0.025$, Appendix 3). We assume that tactile sensitivity is less influenced by the movement speed per se but rather by the difference in impulse caused by the collision with the ball, possibly through a masking mechanism that hinders the detection of the brief probe stimulus, similar to what has been suggested before (Abramsky et al., 1971; Kirman, 1984). To further explore the relationship between the speed of the kicking movement (masking stimulus intensity) and the resulting detection thresholds at around the moment of ball *contact*, we conducted a second experiment.

Experiment 2

The reduction in tactile sensitivity at the kicking foot at the moment of ball *contact* could arise from the phenomenon of tactile masking. This phenomenon occurs when the perception of a tactile stimulus is masked by another stimulus that is presented in close spatial and temporal proximity (Fraser & Fiehler, 2018). Tactile masking can be categorized into three types based on their temporal properties. Forward masking occurs when the masking stimulus precedes the probe stimulus, typically within a window of 70 ms. Simultaneous masking happens when the masking and probe stimuli temporally overlap. Backward masking occurs when the masking stimulus follows the probe stimulus, typically within a window of 100 ms. The strength of forward and backward masking typically decreases with longer stimulus onset asynchrony (Abramsky et al., 1971; Kirman, 1984). In general, the strength of the masking effect is more pronounced when the masking stimulus is more intense (Craig, 1974; Kirman, 1984; Schmid, 1961). In Experiment 2 we explored whether the strong and variable suppression at the moment of ball *contact* found in Experiment 1 is driven by such masking effects irrelevant of any predictive mechanism (Chapman et al., 1987; Fuehrer et al., 2022) or sensory demands (Voudouris & Fiehler, 2021; Wachsmann et al., 2025a) that might be involved. We further tested whether tactile sensitivity at time points shortly before or after the moment of ball *contact* might have been influenced by backward- or forward-masking. To this end, a ball collided in different speeds with the participant's static foot, and we assessed whether tactile sensitivity on that foot is influenced by the ball's speed.

Methods Experiment 2

Participants and apparatus

We recruited again 23 young (22.04 ± 1.77 years old, range: 19-27; height: 176.09 ± 11.86 cm; 13♀, 10♂) healthy participants. None of them had participated in Experiment 1. The inclusion criteria, apparatus, procedure and analysis are identical to those of Experiment 1, except the details mentioned below. This time we had only one tactor at the right (receiving) foot to examine the masking effect of the collision. We also equipped the beam with 3 additional markers (one over the hanging for the ball, and two along the beam) to calculate the angle between beam and the ball. This was necessary to adjust the collision impulse. In addition, we built a cardboard blind to block participants' view of the ball and of the experimenter. This measure was taken to ensure that no predictions about the speed of the ball and the timing of its contact with the foot could be established based on visible ball kinematics. A schematic depiction of the setup is provided in Figure 4.

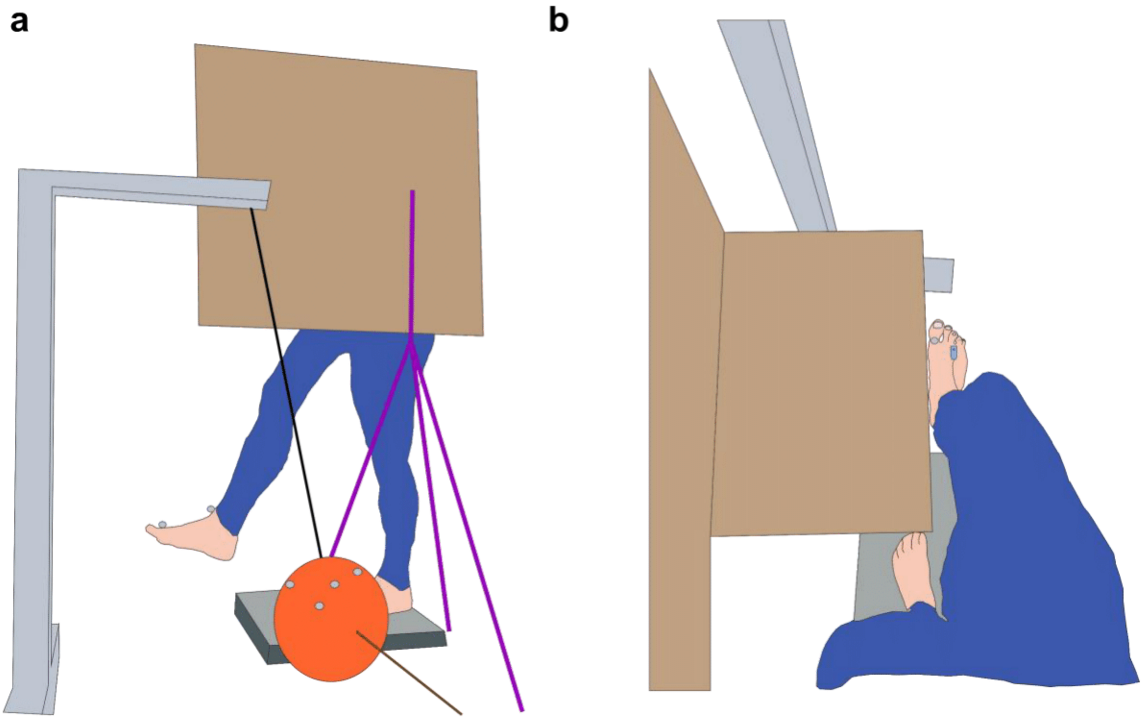

Figure 4: ***Setup Experiment 2.*** *(a) Side view of the setup (experimenter's perspective) showing the beam with the suspended ball, the purple tripod with the occluder attached, a participant standing in the experimental posture, and the four markers on the ball as well as two foot markers. (b) Top view (participant's view) with the occluder covering the ball and its possible trajectory during the experiment. Only one marker and the tactor are visible from this angle.*

Procedure

This experiment comprised four blocks of trials: Sitting baseline, standing baseline, high speed, and low speed. The familiarization phase as well as the determination of the minimal foot-ball distance were identical to Experiment 1.

Participants were randomly assigned to one of eight block sequences. These were all combinations of block orders with the restriction that both baseline conditions had to be presented either before or after the two moving conditions. The sequences were balanced across participants using a block-randomized design to ensure equal representation of the sequences.

In the sitting baseline, participants were seated with both feet in contact with the ground. This was done to preserve the correspondence with Experiment 1. In the standing baseline, participants stood in a posture consistent with the experimental conditions, holding their right foot elevated above the ground in front of them, at approximately the same position where it would collide with the moving ball (ca. 15 cm above ground; Figure 4). We introduced the standing baseline to control for any tactile modulation arising due to the postural demands or due to motor commands reducing sensitivity, therefore reducing the observed effects to the impact of the ball. We introduced breaks of 2-3 sec between trials of the standing baseline block, during which participants adopted a bipedal stance to rest.

For each experimental block (high and low speed), participants performed five practice trials to familiarize themselves with the ball speeds used: either 1500 mm/s or 2500 mm/s. These speeds correspond approximately to the 25th (1742 mm/s) and 75th (2579 mm/s) percentiles of contact speeds observed in Experiment 1 (see Results-Kinematics in Experiment 1). During the practice trials, participants were instructed to lift their right foot to the position in the air aligned with the edge of the occlude in medio-lateral dimension (Figure 4b), where the ball would make contact with it. Each trial started when the experimenter providing a verbal cue, which requested the participants to adopt the necessary leg posture. To achieve the desired ball speed, the experimenter had to lift the ball to a certain angle and then release it. Release height was variable and was adjusted on a trial-by-trial basis since the smoothness of ball release, exact foot placement, and exact rope lengths were slightly variable. Resulting speeds of the ball at the moment of *contact* can be seen in Figure 5b. Meanwhile, it was important that participants could not predict when the ball would start moving toward their foot and from what height, because otherwise they could establish predictions about the timing and intensity of collision, which might influence tactile sensitivity. To prevent the participant from engaging in predictive behavior based on knowing the exact timing of the ball's collision, the experimenter and the ball's starting position were hidden behind an occluder positioned to the participant's left (Figure 4). An auditory signal was delivered to the experimenter via in-ear earplugs to assist the experimenter in positioning the ball at the specific height so that, upon release, it would travel from the participant's left side and collide with the inner part of their foot at the desired target speed (1500 or 2500 mm/s). This initial angle was determined through prior piloting and was adjusted trial-by-trial as necessary to achieve the desired speed. As soon as the experimenter placed the ball at the suitable angle relative to the beam, a continuous auditory signal was delivered to the experimenter's in-ear headphones to inform her that the ball is at the right place. This signal could not be heard by the participant. The experimenter then released the ball. Ball-foot contact was defined as the point at which the ball was within 1.5 cm of the previously established minimum ball-foot distance. At that moment, an intense vibrotactile probe (0.632 mm) was delivered to help participants understand the trial structure. These five practice trials of each experimental block also served to determine the ball's position 235 ms prior to contact for each speed condition, using the averaged data from these trials. This was important for having valid estimates of the *before* time point during the experimental trials and being able to have the *before* condition as a first trial, as it had been done in earlier studies (Arikan et al., 2021; Gertz et al., 2017).

The timing of 235 ms before contact was selected as it corresponded to the median stimulation time (236 ms) observed during the swing phase in Experiment 1. In each of the two experimental blocks, vibrotactile stimulation was randomly administered at one of three time points: *before* contact (-235 ms), at contact, or *after* contact (+250 ms). These time points approximated the phases of *swinging*, *contact*, and *after*-contact used in the first experiment.

As in the practice trials, during the experimental blocks, participants were instructed to hold their right foot elevated in front of them after receiving the experimenter's signal and to wait for the ball to make contact with it. After each trial, participants were asked to indicate whether they perceived the stimulation. Stimulation intensity was decided using the same procedure as in the first experiment. Participants were encouraged to take a bipedal stance between trials to avoid fatigue.

With two ball speeds, three stimulation time points, and two baseline conditions, the experiment involved eight conditions, each managed by a separate QUEST algorithm. Each algorithm required 25 trials, resulting in a total of 200 trials per participant. Experiment 2 lasted approximately 30 min.

Data analysis

As a first step in our analyses, we wanted to ensure that participants kept minimal foot movements around the time of ball contact. This was important to isolate possible effects of the collision between ball and foot from possible effects of moving the foot, as the former effects are related to masking whereas the latter can be related to sensorimotor processes, such as predictions stemming from motor commands associated with the active movement. To this end, we first calculated the maximal foot displacement during the 300 ms before ball contact (Figure 5a). We express this displacement relative to the foot mean position over the same period. Specifically, for each trial, we calculated the maximal 3D distance between the foot and the average foot position during the 300 ms before the ball contacted the foot. We then computed the median across all trials per participant. Additionally, we determined the actual timing of stimulation for each of the three time points of stimulation (*before*, at *contact*, *after*). This resulted in (mean ± standard deviation) -0.245 ± 0.199 ms, 0 ± 0 ms, and 0.252 ± 0.003 ms for the *before*, at *contact*, and *after* time points, respectively. Lastly, we verified whether the achieved and desired speeds at *contact* matched by differentiating the central ball position calculated from the 4 ball markers and computing the Euclidean norm across the three spatial dimensions (Figure 5b).

For the psychophysical analysis, we normalized the data to account for individual differences by subtracting the detection threshold obtained during the standing baseline from those estimated in each of the six experimental conditions. Hereby, we eliminated the influence that is associated with standing and elevating the foot. No participant was excluded from statistical testing.

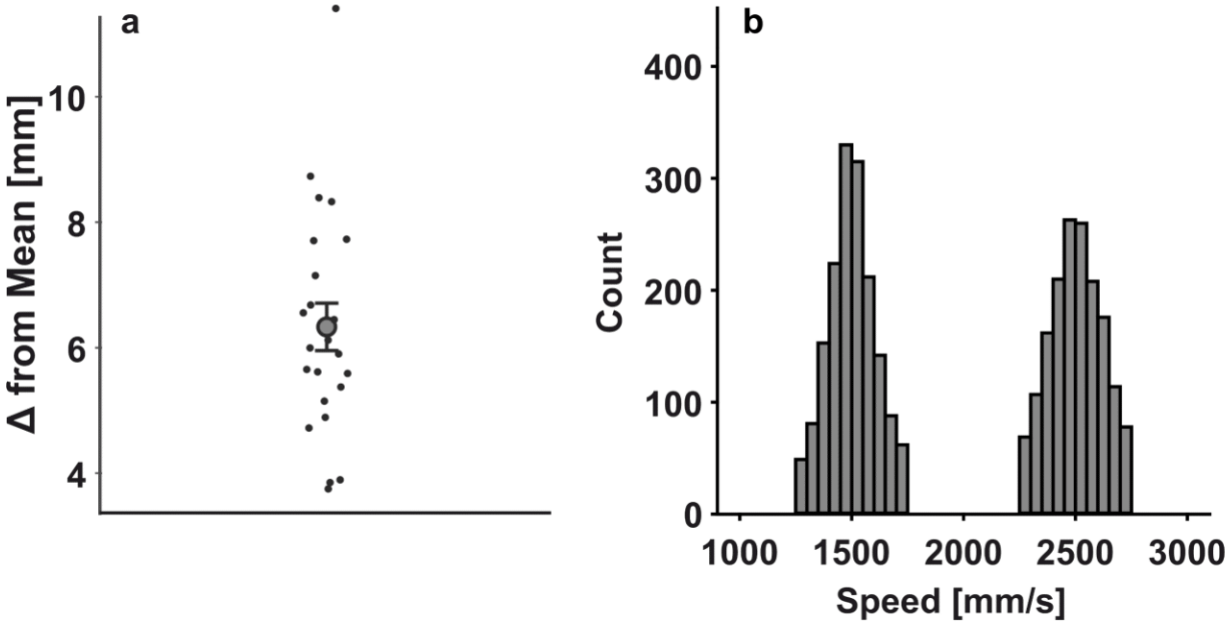

Figure 5: ***Paradigm analysis.*** *(a) Maximal foot displacement to the mean position during the last 300 ms prior to ball contact averaged over all participants. Medians of single participants are depicted by single dots. The error bar shows the standard error while the circle indicates the mean. (b) Distribution of the ball speeds over all trials at the moment of contact.*

Statistical analysis

To assess whether the contact speed and the timing of stimulation influence tactile sensitivity on the static foot, we conducted a 2 (ball speed: slow, fast) × 3 (stimulation timing: *before, contact, after*) repeated-measures ANOVA. Additionally, to investigate whether higher stimulus intensity—expressed in this experiment as different ball impulses—led to greater tactile masking, we performed a one-sided paired-sample t-test on the normalized detection thresholds at the moment of *contact*. The other two time points were not analyzed this way, as they fall outside the temporal window where tactile masking has previously been reported (Abramsky et al., 1971; Kirman, 1984). To test if this is true in our dataset we conducted 2 frequentist and Bayesian paired t-tests between the 2 levels of ball speed intensities that could cause masking. If there was no effect of masking we would assume a Bayes Factor (BF_{0+}) null versus alternative hypothesis above 3, following common recommendations (Andraszewicz et al., 2015) and p values exceeding the conventional threshold of 0.05. We also calculated a paired samples t-test to confirm and replicate an earlier finding that standing itself caused suppression compared to sitting (Wachsmann et al., 2025b).

Results Experiment 2

The 2x3 repeated measure ANOVA confirmed the hypothesized main effect of time ($F_{2,44} = 63.455$, $p < 0.001$, $\eta^2 = 0.743$; Figure 6) and an interaction of time and masking stimulus intensity ($F_{2,22} = 4.139$, $p = 0.023$, $\eta^2 = 0.158$) that arose because suppression at ball *contact* was higher when the ball speed was higher than lower ($t_{22} = 1.909$, $p = 0.035$, $\eta^2 = 0.038$) while no differences were observed in the other two time points (both $p > 0.33$ and $BF_{0+} > 3.152$). The main effect of masking stimulus intensity (ball speed) did not reach significance ($F_{2,44} = 2.406$, $p = 0.135$ $\eta^2 = 0.099$). Detection thresholds at baseline were significantly higher in standing than sitting, as expected ($t_{22} = 2.672$, $p = 0.007$, $\eta^2 = 0.072$).

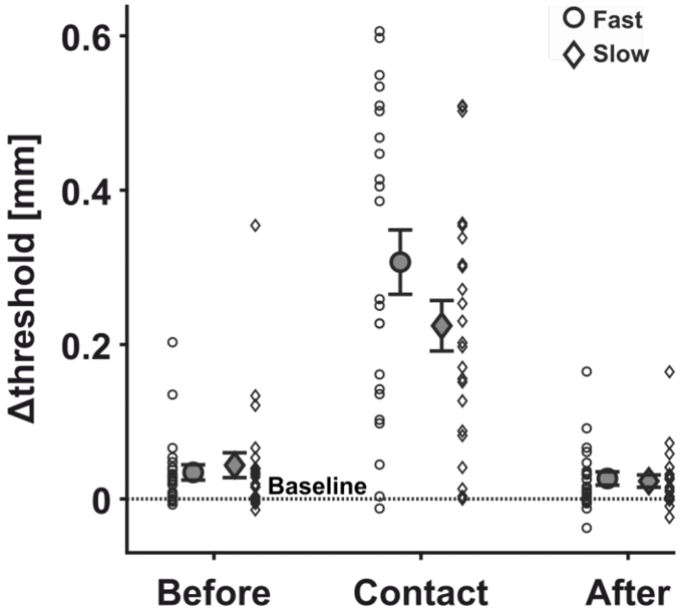

Figure 6: ***Psychophysical results.*** *Detection thresholds during experimental trials normalized to the standing baseline (Δthreshold) at the three time points of stimulation relative to ball contact. Single subject data are depicted as small symbols (circle for fast and diamonds for slow ball velocities) while big symbols with error bars represent the means and standard errors. The dashed line shows baseline performance.*

Discussion Experiment 2

In the second experiment, we aimed to test whether tactile processing in the lower limbs is influenced by peripheral processes, such as tactile masking, which might explain the pronounced and variable suppression at the time of ball *contact*, and possibly adjacent time points, in Experiment 1. To do so, participants held their static foot in the air without visual information about a ball that approached their foot with two different speeds. We again applied tactile stimuli at three different time points.

As expected (Abramsky et al., 1971), we observed a clear increase in tactile detection thresholds at the time of ball *contact* compared to the time points *before* and *after* contact. This suggests that tactile sensitivity at *contact* is strongly influenced by masking. We did not find a main effect of masking stimulus intensity, which is unsurprising given that the *before* and *after* time points were outside the typical temporal ranges for forward and backward masking (Abramsky et al., 1971; Kirman, 1984). We could statistically confirm that the *before* and *after* time points were not due to ball contact-dependent masking, since the impulses did not influence tactile sensitivity. More importantly, we found a significant interaction between time point and ball speed, which is driven by suppression being larger when the ball contacted the foot with higher than lower speeds. This interaction highlights the fact that the influence of masking stimulus intensity on tactile sensitivity is most pronounced during ball *contact*, underscoring the temporal specificity of the masking phenomenon.

These findings indicate that tactile masking may have contributed to the pronounced suppression at the moment of ball *contact* observed in Experiment 1. However, more factors are likely involved in that finding, such as the precise prediction about when and how quickly the kicking foot would hit the ball. Indeed, more reliable predictions about the sensory consequences of one's own action lead to stronger suppression (Blakemore et al., 1999; Fuehrer et al., 2022). Tactile masking at the foot during collisions with a ball is modulated by the masking stimulus intensity, and this occurs within a similar time window to that reported in the upper limbs (Craig, 1974; Fraser & Fiehler, 2018; Kirman, 1984; Schmid, 1961). We speculate that masking generalizes throughout the leg since reduction in tactile sensitivity also appears at the calf when postural sways are larger (Wachsmann et al., 2025b).

Summary

In summary, we demonstrate that tactile sensitivity in the lower limbs is dynamically modulated during complex, everyday movements and that this modulation resembles those observed in upper limb goal-directed movements. In Experiment 1, we identified a distinct pattern in the kicking leg**:** tactile sensitivity increased from movement *onset* to the *swing* phase—when guiding demands are highest—followed by pronounced suppression at ball *contact* and a subsequent recovery of sensitivity**.** In contrast, tactile sensitivity was suppressed in the balancing foot during the kicking's leg *swing* phase, with recovery thereafter. Notably, this suppression did not align with the peak foot speed**,** which occurs around movement *onset* of the kicking leg, suggesting that postural demands rather than movement speed primarily drive the modulation (Cybulska-Klosowicz et al., 2011).

Across both experiments, tactile suppression at the moment of ball *contact* scaled with contact impulse. Experiment 2 confirmed that this effect occurs within a narrow temporal window, as tactile sensitivity during the *before* and *after* time points was not substantially affected. This strengthens our confidence in the observed magnitudes of modulation effects of the first experiment. Together, two tactile sensitivity modulation patterns were observed in the different feet, suggesting that tactile modulation is governed by two main mechanisms: tactile sensitivity can be upweighted at moments when online feedback from the probed limb is important for the action (Colino & Binsted, 2016; Voudouris et al., 2019; Voudouris & Fiehler, 2022), while postural demands (Wachsmann et al., 2025b) and masking (Abramsky et al., 1971; Kirman, 1984) reduce it.

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Fabian Dominik Wachsmann (Fabian.wachsmann@psychol.uni-giessen.de)

Data availability

Behavioral and psychophysical data are publicly available after acceptance at osf.io/bvtdk. For further information or data requests please correspond to Fabian Dominik Wachsmann (Fabian.Wachsmann@psychol.uni-giessen.de).

Author contributions

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Formal analysis: F.W.

Funding acquisition: K.F., D.V.

Investigation: F.W.

Methodology: F.W., K.F., D.V.

Project administration: F.W., K.F., D.V.

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Supervision: K.F., D.V.

Validation: F.W., K.F., D.V.

Visualization: F.W.

Roles/Writing - original draft: F.W.

and Writing - review & editing: F.W., K.F., D.V.

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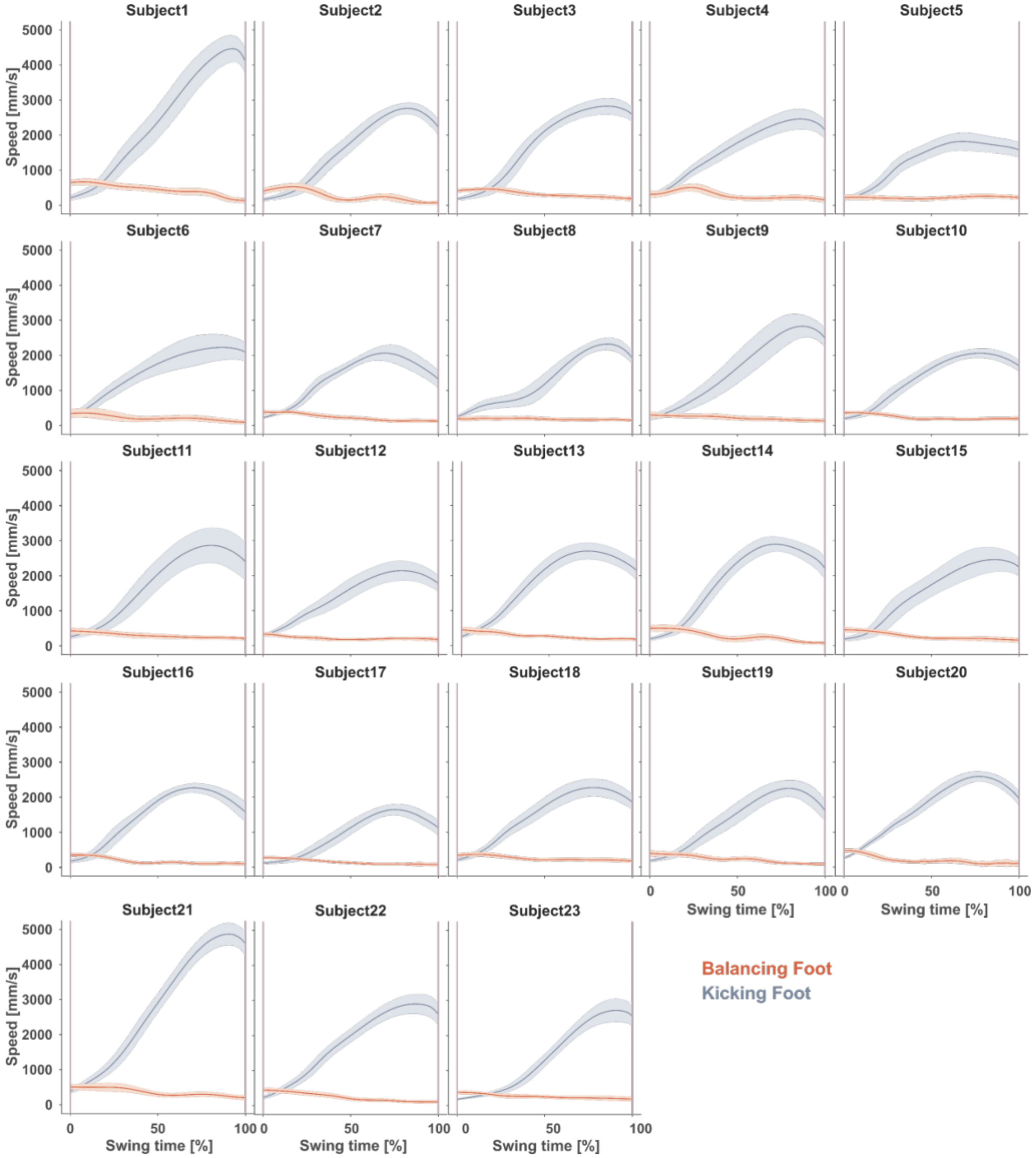
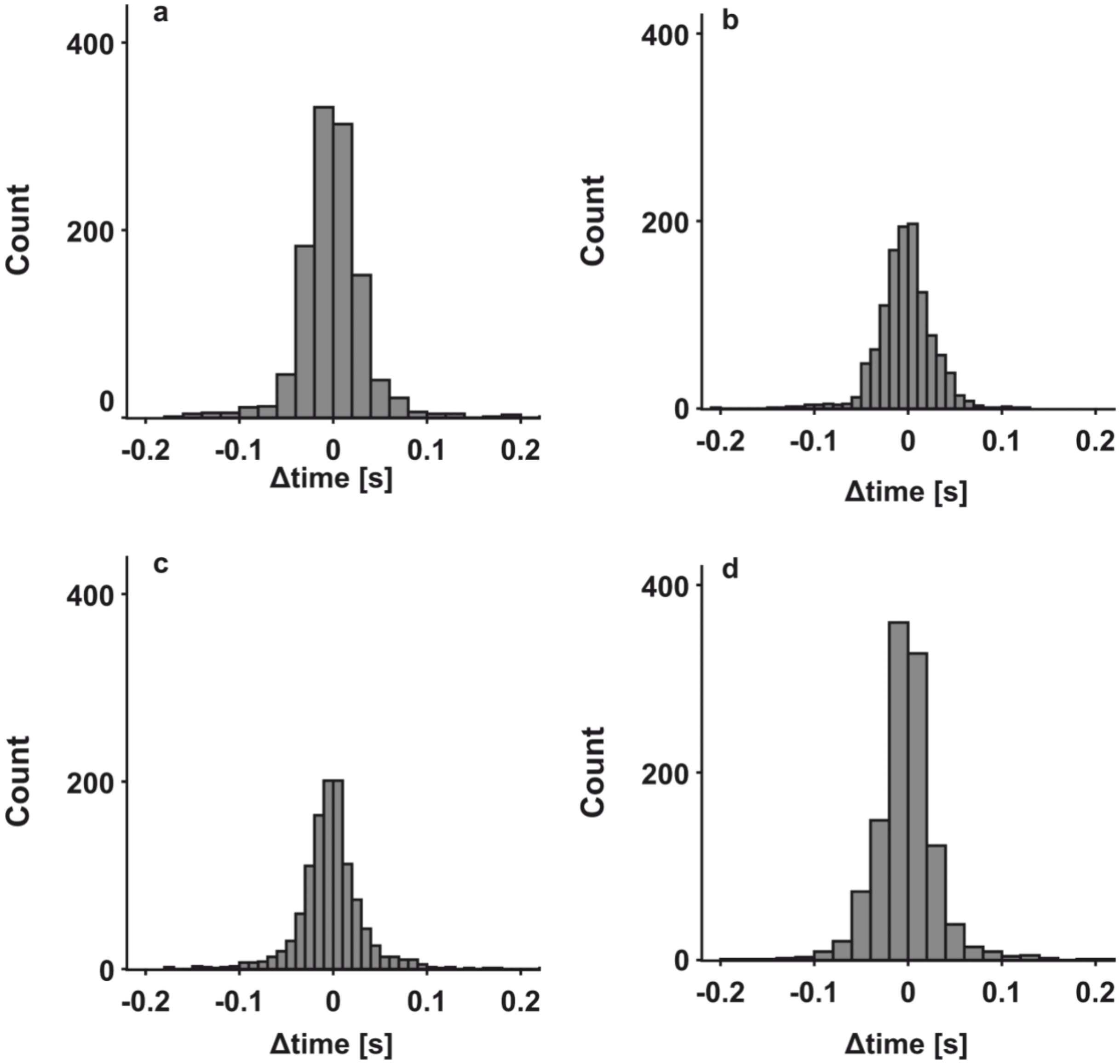
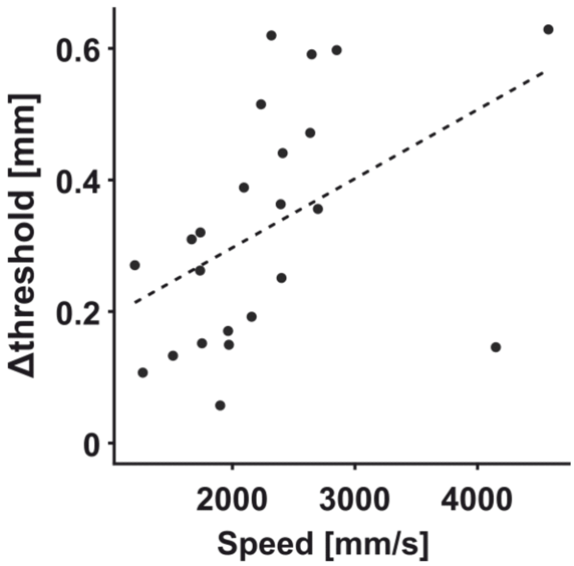
Appendix



Appendix 1: ***Single subject speed profiles.*** *The figure shows the time normalized single subject time-courses of the swinging phase for the kicking (blue) and the balancing (red) leg for all participants, with standard errors as shaded error bars. The first and second purple vertical lines indicate movement onset and moment of ball contact, respectively. Please note that the speed of the balancing leg is decreasing as it reached maximum around the kicking foot movement onset.*



Appendix *2:* ***Differences between intended and actual stimulation.*** *Histograms of the time differences between the intended and the actual vibrotactile stimulation for all trials, separately for the four stimulation time points (a) onset, (b) swing, (c) ball contact, and (d) after-contact.*



Appendix 3: ***Correlation of foot speed and normalized detection threshold.*** *Normalized detection thresholds as a function of the kicking leg's speed at the moment of ball contact. The strength of suppression is expressed as the amplitude of the vibration stimulus difference from baseline. Dots represent single subject data, while the dashed line indicates a first order polynomial fitted to the data.*

4 List of peer-reviewed journal articles

Wachsmann, F. D., Fiehler, K., & Voudouris, D. (2025a). Temporal modulation of tactile perception during balance control. *Scientific Reports*, *15*(1), 17380. https://doi.org/10.1038/s41598-025-99006-8

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Gießen, 15.10.2025 Fabian Dominik Wachsmann